PROCEEDINGS

OF THE

AMERICAN PHILOSOPHICAL SOCIETY

HELD AT PHILADELPHIA

FOR PROMOTING USEFUL KNOWLEDGE

VOL. LII MAY–AUGUST, 1913 No. 210

THE ALLEGHENIAN DIVIDE, AND ITS INFLUENCE UPON THE FRESHWATER FAUNA.

(PLATES XII–XIV.)

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(*Read April 18, 1913.*)

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INTRODUCTION.

It is a well-known fact, noticed already by Rafinesque, in 1820 (Monogr. Coqu. Biv. et Fluv.), that the Appalachian Mountain system forms, for many freshwater animals, a sharp faunistic division line, which separates a fauna known as that of the *Interior Basin* from that of the *Atlantic Slope* (Mississippian and Atlantic Region

of Simpson, 1893, p. 354, and 1900a, p. 505, pl. 18). But it should be noted, from the beginning, that this holds good only for certain groups of animals, while in others no such differentiation is observed.

While this appears to be correct in a general way, investigations on the details of the relations of the two faunas on the eastern and the western side of the Alleghenies are very few. In fact, there are none whatever that have treated this question from a broader viewpoint. The most elementary requirement, the study of the actual distributional facts of freshwater animals, had been greatly neglected. From most of the more important rivers (Susquehanna, Potomac, Allegheny, Monongahela, Kanawha) hardly any observations were at hand, which would have permitted any definite opinion as to the general character of their faunas, and in the region of the headwaters of these, our previous knowledge was a blank.

For this reason, the present writer had first of all to undertake the task of obtaining reliable and complete data with regard to the fauna of the various streams running off the Alleghenian divide. In the course of these studies it became evident that the most important group of freshwater life is formed by the *Najades* or *Freshwater Mussels*. They offer two advantages: first they are very rich in species, the natural affinities of which are now rather clear; and second, they are forms which apparently possess no exceptional means of dispersal, that is to say, they are, as a rule, unable to cross from one drainage system into another over land (either actively or passively). This opinion of mine agrees with that held by Simpson (1900b), but is in sharp contrast to that expressed by Johnson (1905), who believes that "shells" or "mollusks" in general, and also especially Najades, have frequently been dispersed by birds, etc. Such cases may happen among the Najades, but they cannot be considered as the normal way, and Johnson's view rests upon very inadequate ideas about Najad-distribution, and chiefly the instances of apparent discontinuous distribution of species, which would favor the assumption of transport, are, without exception, founded upon defective facts. (It should be remembered that the chief means of dispersal of the Najades consists of transport in the larval state by fishes, on which the larvæ are attached; but this precludes the possibility of transport over land.)

Thus the present paper treats in the first line of the *Najades.* But there are other groups, which are important, yet they will be interesting only in so far as they confirm the results obtained from the Najades. These are certain freshwater *Gastropods,* and the crayfish-genus *Cambarus.* However, in the Gastropods we are handicapped by an insufficient knowledge of their mutual natural affinities; and in the Crayfishes the number of forms, which are to be considered, is rather small, so that it would be difficult to obtain general results from them alone.

In the present paper, the writer is going to pay attention only to that part of the Alleghenian divide which lies between the New York–Pennsylvania state line and the northern line of Tennessee (see Plate XII.). In the north we have a rather natural boundary: from about the New York state line northward the Glacial area begins, offering geological and physiographical features which are of rather recent age, and have created special conditions, which should be investigated separately. In the south, in the region of the headwaters of the Tennessee drainage, the conditions form the continuation of those farther north, but become here so complex that they deserve special study, to which additional, and much more extended investigations are necessary, involving the "Tennessee-Coosa problem."[1] I have considered the upper Tennessee only so

[1] This is the problem in which Johnson (1905) is especially interested. The old idea is (see chiefly Hayes, 1899) that the headwaters of the Tennessee once continued in the direction of the Coosa (*Appalachian River*), and that the present course of the Tennessee is due to a deflection in consequence of stream capture. Johnson believes (and also White, 1904) that the present course of the Tennessee is original, and I consider his physiographical evidence as perfectly sound and satisfactory. But since the Najades (and other freshwater groups) have been used to demonstrate the correctness of the assumption of the existence of the Appalachian River (see: Simpson, 1900b, p. 133, Adams, 1901, p. 846, and Ortmann, 1905, p. 130), we must take cognizance of this line of evidence, and dispose of it in some way. Johnson did this by dismissing it as not convincing, as not apt to demonstrate stream capture. However, as I have said, he is wrong in this, and I believe that the distribution of the Najades *does indicate stream capture in this region,* but in the opposite direction: the original fauna belonged to the old Tennessee (similar to the present in its course), and certain southern tributaries of it have been captured by the Coosa-Alabama system. This idea is already implied in Simpson's (1900b, p. 135) sentence: "it is probable that nearly all the

far as to ascertain the great contrast which exists between it and the river systems to the north of it. Thus my investigations cover, on the western side of the Alleghenies, the drainages of the Allegheny and Monongahela rivers (upper Ohio), of the Kanawha River, and in part only of the Big Sandy, Licking and Tennessee rivers (Clinch and Holston). On the eastern side, the systems of the Delaware, Susquehanna, Potomac, and of the upper James and Roanoke are included.

It is believed that the faunistic facts with regard to these rivers are reasonably complete and that my collections in them have furnished the knowledge, not only of what is present in them, but also of what is absent; under circumstances, this latter fact may even be more valuable than positive records.

Chapter I.

Statement of Distributional Facts in Najades.

The nomenclature of the Najades is that introduced by myself in some recent publications (chiefly Ortmann, 1912a, pp. 222 ff.). The lists give the number of distinguishable forms, no matter whether they are species or varieties. Unless otherwise stated, all information is founded upon the writer's personal experience, and the specimens from the various localities are preserved in the collections of the Carnegie Museum in Pittsburgh. The great mass of new distributional facts secured by the writer makes it imperative to give them in full. For this reason, the present chapter is somewhat lengthy and contains much that is uninteresting reading for those which are not specialists. But this is unavoidable.

A. WESTERN SIDE OF ALLEGHENIES.

I. The Upper Ohio Fauna in General.

First I give a complete list of species (or forms) found in the upper Ohio drainage, above Smith Ferry, Beaver Co., Pa., in the

Unionidæ of the Alabama River system have been derived from the Tennessee," and White (1904, p. 38) directly says that the upper course of the original Walden Gorge River (tributary to Tennessee) has been captured by Conasauga River (tributary to Oostanaula and Coosa Rivers).

Ohio, Allegheny, Monongahela Rivers, and their tributaries, excluding those found only in the Beaver or French Creek systems (Glacial Drift streams).[2]

List No. 1.

1. *Fusconaia subrotunda* (Lea)
2. *Fusconaia undata trigona* (Lea)
3. *Fusconaia undata rubiginosa* (Lea)
4. *Crenodonta plicata undulata* (Barn.)
5. *Quadrula pustulosa* (Lea)
6. *Quadrula lachrymosa* (Lea)
7. *Quadrula tuberculata* (Barn.)
8. *Quadrula metanevra* (Raf.)
9. *Quadrula cylindrica* (Say)
10. *Rotundaria tuberculata* (Raf.)
11. *Plethobasus cooperianus* (Lea)
12. *Plethobasus cyphus* (Raf.)
13. *Pleurobema obliquum* (Lamarck)
14. *Pleurobema obliquum pyramidatum* (Lea)
15. *Pleurobema obliquum coccineum* (Conr.)
16. *Pleurobema clava* (Lam.)
17. *Elliptio crassidens* (Lam.)
18. *Elliptio dilatatus* (Raf.)
19. *Symphynota compressa* Lea.
20. *Symphynota costata* (Raf.)
21. *Hemilastena ambigua* (Say)
22. *Anodonta grandis* Say
23. *Alasmidonta marginata* (Say)
24. *Strophitus edentulus* (Say)
25. *Ptychobranchus phaseolus* (Hildr.)
26. *Obliquaria reflexa* Raf.
27. *Cyprogenia irrorata* (Lea)

[2] Forms peculiar to Beaver or French Creek (or both) are: *Fusconaia subrotunda kirtlandiana* (Lea), *Symphynota complanata* (Barnes), *Anodonta imbecillis* Say, *Anodontoides ferussacianus* (Lea), *Carunculina parva* (Barnes).

Symphynota compressa Lea probably also falls in this category, but is also found in the uppermost Allegheny.

28. *Obovaria retusa* (Lam.)
29. *Obovaria circulus* (Lea)
30. *Obovaria circulus lens* (Lea)
31. *Obovaria ellipsis* (Lea)
32. *Nephronaias ligamentina* (Lam.)
33. *Amygdalonaias elegans* (Lea)
34. *Amygdalonaias donaciformis* (Lea)
35. *Plagiola depressa* (Raf.)
36. *Paraptera gracilis* (Barn.)
37. *Proptera alata* (Say)
38. *Eurynia fabalis* (Lea)
39. *Eurynia iris* (Lea)
40. *Eurynia recta* (Lam.)
41. *Lampsilis luteola* (Lam.)
42. *Lampsilis ovata* (Say)
43. *Lampsilis ovata ventricosa* (Barn.)
44. *Lampsilis multiradiata* (Lea)
45. *Lampsilis orbiculata* (Hildr.)
46. *Truncilla triquetra* (Raf.)
47. *Truncilla perplexa rangiana* (Lea)

It should be noted, that, of these, six forms (nos. 6, 11, 28, 31, 33, 34) have been found exclusively in the Ohio below Pittsburgh, while nine forms (nos. 3, 15, 16, 19, 25, 30, 38, 39, 47) have not been found there, but only above Pittsburgh, but they are found elsewhere in the Ohio drainage, so that they are not restricted to this region. No. 21 has been found only once, in the headwaters of the Monongahela, in West Fork River, in Lewis Co., W. Va. Thus there are *37 forms in the Ohio below Pittsburgh.*

II. Lower Allegheny and Monongahela Rivers.

There are, in the *Allegheny River* above Pittsburgh and below Franklin, Venango Co., Pa., the following Najades.

List No. 2.

1. *Fusconaia subrotunda* (Lea)
2. *Fusconaia undata rubiginosa* (Lea)

3. *Crenodonta plicata undulata* (Barn.)
4. *Quadrula pustulosa* (Lea)
5. *Quadrula tuberculata* (Barn.)
6. *Quadrula metanevra* (Raf.)
7. *Quadrula cylindrica* (Say)
8. *Rotundaria tuberculata* (Raf.)
9. *Plethobasus cyphyus* (Raf.)
10. *Pleurobema obliquum* (Lam.)
11. *Pleurobema obliquum pyramidatum* (Lea)
12. *Pleurobema obliquum coccineum* (Conr.)
13. *Pleurobema clava* (Lam.)
14. *Elliptio crassidens* (Lam.)
15. *Elliptio dilatatus* (Raf.)
16. *Symphynota costata* (Raf.)
17. *Alasmidonta marginata* (Say)
18. *Strophitus edentulus* (Say)
19. *Cyprogenia irrorata* (Lea)
20. *Obovaria circulus lens* (Lea)
21. *Nephronaias ligamentina* (Lam.)
22. *Plagiola depressa* (Raf.)
23. *Paraptera gracilis* (Barn.)
24. *Proptera alata* (Say)
25. *Eurynia recta* (Lam.)
26. *Lampsilis luteola* (Lam.)
27. *Lampsilis ovata* (Say)
28. *Lampsilis ovata ventricosa* (Barn.)
29. *Lampsilis multiradiata* (Lea)
30. *Lampsilis orbiculata* (Hildr.)
31. *Truncilla triquetra* (Raf.)
32. *Truncilla perplexa rangiana* (Lea)

Aside from the six species found only below Pittsburgh, the following nine of list no. 1 are missing here: nos. 2, 19, 21, 22, 25, 26, 29, 38, 39.

A very similar fauna goes up the *Monongahela River*. Unfortunately, this fauna is now destroyed, and our knowledge of it rests upon a collection in the Carnegie Museum made before 1897 by

G. A. Ehrmann in the vicinity of Charleroi, Washington Co., Pa. (and a few scattered additional records secured by others). The following is the list of these.

List No. 3.

1. *Fusconaia subrotunda* (Lea)
2. *Fusconaia undata trigona* (Lea)
3. *Fusconaia undata rubiginosa* (Lea)
4. *Quadrula pustulosa* (Lea)
5. *Quadrula tuberculata* (Barn.)
6. *Quadrula metanevra* (Raf.)
7. *Quadrula cylindrica* (Say)
8. *Plethobasus cyphyus* (Raf.)
9. *Pleurobema obliquum* (Lam.)
10. *Pleurobema obliquum pyramidatum* (Lea)
11. *Elliptio crassidens* (Lam.)
12. *Elliptio dilatatus* (Raf.)
13. *Symphynota costata* (Raf.)
14. *Anodonta grandis* Say
15. *Strophitus edentulus* (Say)
16. *Ptychobranchus phaseolus* (Hildr.)
17. *Obliquaria reflexa* Raf.
18. *Cyprogenia irrorata* (Lea)
19. *Obovaria circulus* (Lea)
20. *Obovaria circulus lens* (Lea)
21. *Nephronaias ligamentina* (Lam.)
22. *Plagiola depressa* (Raf.)
23. *Paraptera gracilis* (Barn.)
24. *Proptera alata* (Say)
25. *Eurynia recta* (Lam.)
26. *Lampsilis luteola* (Lam.)
27. *Lampsilis ovata ventricosa* (Barn.)
28. *Lampsilis orbiculata* (Hildr.)

The following species have not been found here, but were probably present in this region, since they exist both below and above:

29. *Crenodonta plicata undulata* (Barn.)
30. *Rotundaria tuberculata* (Raf.)
31. *Alasmidonta marginata* (Say)
32. *Lampsilis multiradiata* (Lea)
33. *Truncilla triquetra* (Raf.)

Comparing these two lists (nos. 2 and 3), we see that they are practically identical: 23 forms are in either list, to which probably five others should be added, which should be expected in this part of the Monongahela. Thus there would be 28 forms common to these rivers.

Even those species, which are peculiar to only one of these rivers, might exist or might have existed in the other. In a general way, those species found in the Monongahela, and not in the Allegheny, are preëminently big-river-forms (for instance *Fusc. undata trigona, Obliquaria reflexa, Obovaria circulus*), while, vice versa, those of the Allegheny are small-river-forms (*Pleurobema obliquum coccineum, Pleurobema clava, Truncilla perplexa rangiana*). This is in keeping with the general character of these rivers; the Monongahela is, although not appreciably larger, more quiet and steady, with finer bottom (gravel, sand), while the Allegheny is rather rough, with coarser gravel and rocks.

One thing is very evident: that the Ohio fauna extends into both rivers above Pittsburgh, but somewhat depauperated, decreasing from 37 to about 30 Najad-forms.

III. The Upper Allegheny and its Tributaries.

Going up the Allegheny River, we meet first a section, which is utterly polluted (from northern Armstrong Co., to Oil City, Venango Co.). But above Oil City the river is in good condition, up to Warren Co., and the New York state line. In this stretch (Venango, Forest, and Warren Cos.), the following Najades have been collected by the writer:

List No. 4.

1. *Crenodonta plicata undulata* (Barn.)
2. *Rotundaria tuberculata* (Raf.)

3. *Pleurobema obliquum coccineum* (Conr.)
4. *Pleurobema clava* (Lam.)
5. *Elliptio dilatatus* (Raf.)
6. *Symphynota costata* (Raf.)
7. *Alasmidonta marginata* (Say)
8. *Strophitus edentulus* (Say)
9. *Ptychobranchus phaseolus* (Hildr.)
10. *Nephronaias ligamentina* (Lam.)
11. *Eurynia fabalis* (Lea)
12. *Eurynia recta* (Lam.)
13. *Lampsilis ovata* (Say)
14. *Lampsilis ovata ventricosa* (Barn.)
15. *Lampsilis multiradiata* (Lea)
16. *Truncilla perplexa rangiana* (Lea)

To these should be added, as found in tributaries of the Allegheny in Warren Co.:

17. *Symphynota compressa* Lea
18. *Anodonta grandis* Say
19. *Lampsilis luteola* (Lam.)

Compared with the lower Allegheny (list no. 2), the number of species has been reduced by more than a third, but for those which have disappeared a few others have turned up, namely, nos. 9, 11, 17 and 18. Of these, *Symphynota compressa* (no. 17) is a peculiar form restricted to the tributaries of the upper Allegheny (and also in French Creek and Beaver River drainage, see above, p. 291, footnote 2). The others are species which generally prefer small streams and avoid larger rivers.

Above Warren Co., Pa., the Allegheny River flows in New York state, and we have only a few records from this section (Marshall, 1895). But then we reach Pennsylvania again in McKean Co. Here I secured a number of species in the Allegheny River, and received others from Dennis Dally, and P. E. Nordgren made a collection in Potato Creek. Here is the list of these.

List No. 5.

(Those marked * are from the *Allegheny,* those marked † from *Potato Creek.*)

*1. *Pleurobema obliquum coccineum* (Conr.)
*†2. *Elliptio dilatatus* (Raf.)
†3. *Symphynota compressa* Lea
*†4. *Symphynota costata* (Raf.)
*5. *Alasmidonta marginata* (Say)
†6. *Strophitus edentulus* (Say)
*†7. *Lampsilis luteola* (Lam.)
*8. *Lampsilis ovata ventricosa* (Barn.)

The number of forms again has been greatly reduced in comparison with list no. 4. All species found here are also found farther below, and thus this fauna is simply depauperated.

I collected also in the uppermost Allegheny above Coudersport, Potter Co., but here this is a mere run, and has no Najades. (Immediately below Coudersport it is polluted.)

We come now to the eastern tributaries of the Allegheny River, running down from the divide in a general east–west direction. They are (from north to south): *Clarion River, Red Bank River, Mahoning Creek, Crooked Creek,* and *Kiskiminetas River.* The first two are entirely polluted, and no shells are known from them. The same is true for Mahoning Creek, from Punxsutawney down. But in northern Indiana Co. there is a tributary of the latter, *Little Mahoning Creek,* where I collected the following shells:

List No. 6.

1. *Pleurobema obliquum coccineum* (Conr.)
2. *Elliptio dilatatus* (Raf.)
3. *Symphynota costata* (Raf.)
4. *Alasmidonta marginata* (Say)
5. *Strophitus edentulus* (Say)
6. *Ptychobranchus phaseolus* (Hildr.)
7. *Lampsilis luteola* (Lam.)
8. *Lampsilis ovata ventricosa* (Barn.)

The similarity of this fauna to that of the uppermost Allegheny is evident. Eight forms are in either list, seven of which are found in both.

Crooked Creek has its fauna fully preserved. I collected in both the lower and upper part. In the lower part, in Armstrong Co., near its confluence with the Allegheny, the following are found.

List No. 7a.

1. *Fusconaia undata rubiginosa* (Lea)
2. *Crenodonta plicata undulata* (Barn.)
3. *Pleurobema obliquum coccineum* (Conr.)
4. *Elliptio dilatatus* (Raf.)
5. *Symphynota costata* (Raf.)
6. *Anodonta grandis* Say
7. *Alasmidonta marginata* (Say)
8. *Strophitus edentulus* (Say)
9. *Obovaria circulus lens* (Lea)
10. *Nephronaias ligamentina* (Lam.)
11. *Eurynia fabalis* (Lea)
12. *Eurynia iris* (Lea)
13. *Eurynia recta* (Lam.)
14. *Lampsilis luteola* (Lam.)
15. *Lampsilis ovata ventricosa* (Barn.)
16. *Lampsilis multiradiata* (Lea)
17. *Truncilla triquetra* Raf.

This is a depauperated lower Allegheny fauna, with the addition of a few species (nos. 6, 11, 12) which are characteristic for smaller streams.

In the upper part of Crooked Creek, in Indiana Co., there are:

List No. 7b.

1. *Fusconaia undata rubiginosa* (Lea)
2. *Symphynota costata* (Raf.)
3. *Anodonta grandis* Say
4. *Strophitus edentulus* (Say)

5. *Obovaria circulus lens* (Lea)
6. *Lampsilis luteola* (Lam.)

This part of the creek is a very small stream. Of the six species found here, three are also in the uppermost Allegheny and in Little Mahoning, while three (nos. 1, 3, 5) are absent in them. *Anodonta grandis* is a small-creek-form elsewhere, but *Fusconaia undata rubiginosa* and *Obovaria circulus lens* are peculiar to this creek, and although they are also small-creek-forms, they are not known to advance so far up toward the divide in other rivers. Of course, we should bear in mind that other tributaries of the Allegheny in this section, the fauna of which has been destroyed, might have contained these species.

The full and typical *Kiskiminetas-Conemaugh* fauna is irreparably lost to us on account of pollution of the waters. However, a few remnants have been preserved. Nothing is known from the Kiskiminetas proper. In the *Conemaugh River* at New Florence, Westmoreland Co., I found the dead shells of the following forms:

1. *Pleurobema obliquum coccineum* (Conr.)
2. *Pleurobema clava* (Lam.)
3. *Elliptio dilatatus* (Raf.)
4. *Ptychobranchus phaseolus* (Hildr.)
5. *Nephronaias ligamentina* (Lam.)
6. *Eurynia recta* (Lam.)
7. *Lampsilis ovata ventricosa* (Barn.)
8. *Lampsilis multiradiata* (Lea)

These are all found in the Allegheny above Oil City, but it is hardly probable that this list contains more than half of the species originally present in the Conemaugh.

From small tributaries in Westmoreland and Indiana Cos., I was able to secure four species:

Elliptio dilatatus (Raf.)—Yellow Creek, Indiana Co.
Symphynota costata (Raf.)—Two Lick Creek, Indiana Co.
Anodonta grandis Say—Beaver Run, Westmoreland Co.
Strophitus edentulus (Say)—Yellow Creek and Blacklegs Creek, Indiana Co., and Beaver Run, Westmoreland Co.

Also this fauna is fragmentary, since these streams are partially polluted. But there are two tributaries of the Kiskiminetas system, in the mountains, between Chestnut Ridge, Laurel Hill Ridge, and Allegheny Front, which have furnished what appears as complete faunas. *Loyalhanna River,* near Ligonier, Westmoreland Co., contains:

List No. 8.

1. *Pleurobema obliquum coccineum* (Conr.)
2. *Pleurobema clava* (Lam.)
3. *Elliptio dilatatus* (Raf.)
4. *Symphynota costata* (Raf.)
5. *Alasmidonta marginata* (Say)
6. *Strophitus edentulus* (Say)
7. *Ptychobranchus phaseolus* (Hildr.)
8. *Lampsilis ovata ventricosa* (Barn.)
9. *Lampsilis multiradiata* (Lea)

Also *Anodonta grandis* Say should be mentioned, but this has been found only in ponds cut off from the river. Of *Nephronaias ligamentina* (Lam.) a single individual has been found many years ago, but recent investigations have failed to bring it to light again.

Seven of these species have occurred in the other lists of the tributaries of the Allegheny, while two are new (nos. 2 and 9).

In *Quemahoning Creek,* in Somerset Co., I collected:

List No. 9.

1. *Elliptio dilatatus* (Raf.)
2. *Symphynota costata* (Raf.)
3. *Alasmidonta marginata* (Say)
4. *Strophitus edentulus* (Say)
5. *Ptychobranchus phaseolus* (Hildr.)
6. *Lampsilis ovata ventricosa* (Barn.)
7. *Lampsilis multiradiata* (Lea)

All these are also found in the Loyalhanna, but two of the latter (nos. 1 and 2) are lacking.

The streams belonging to the Allegheny, discussed so far, form

a unit, as will become evident by comparison with the next group (upper Monongahela drainage). This is the most easterly advanced part of the Allegheny drainage. For this reason it will be advantageous to give the full list of all species which advance here farthest toward the Alleghenian divide.

Combined Lists: 6, 7b, 8, 9.

1. *Fusconaia undata rubiginosa* (Lea)
2. *Pleurobema obliquum coccineum* (Conr.)
3. *Pleurobema clava* (Lam.)
4. *Elliptio dilatatus* (Raf.)
5. *Symphynota compressa* Lea
6. *Symphynota costata* (Raf.)
7. *Anodonta grandis* Say
8. *Alasmidonta marginata* (Say)
9. *Strophitus edentulus* (Say)
10. *Ptychobranchus phaseolus* (Hildr.)
11. *Obovaria circulus lens* (Lea)
12. *Lampsilis luteola* (Lam.)
13. *Lampsilis ovata ventricosa* (Barn.)
14. *Lampsilis multiradiata* (Lea)

This is a comparatively rich fauna. Although not all of these 14 species are found in every one of these streams, the average number is about 7 or 8. Some of the species (*Symphynota costata, Strophitus edentulus*) are found in all of these creeks, and five species are in most of them (*Pleurobema obliquum coccineum, Elliptio dilatatus, Alasmidonta marginata, Ptychobranchus phaseolus, Lampsilis ovata ventricosa*).

Looking over the Allegheny River fauna, we see that the Ohio fauna, well and richly represented in the Ohio below Pittsburgh by 37 forms, depauperates in the Allegheny. Although a few species are added toward the headwaters, the general tendency is that one species after the other disappears in the upstream direction. But one feature of this should be emphasized: the decrease in the number of forms is *gradual,* no sudden deterioration of the fauna being

observed at any point. In the uppermost headwaters there is yet a comparatively rich fauna of together 14 species.

We shall see that in other parts of the western drainage this condition is not found, and our rather detailed account of the Allegheny fauna has been given with the chief purpose of bringing out the above fact.

IV. Monongahela River and Tributaries.

We have seen above (list no. 3) that the Monongahela just above Pittsburgh had surely 28 species, but possibly 33. Farther up no Najades are known and the fauna is destroyed, for the water is everywhere badly polluted. But above Clarksburg, Harrison Co., W. Va., conditions are good again in *West Fork River*. This is a Plateau stream, not rough, but rather sluggish, and the proper environment for shell-life seems to be present. The Carnegie Museum possesses material collected by the writer at Lynch Mines, Harrison Co., at Lightburn and Weston, Lewis Co., and some additional forms collected by J. P. Graham at West Milford, Harrison Co., W. Va. This gives us a good, and, as I believe, a rather complete idea of this fauna.

In the following list those forms found at the uppermost point in this river (Weston) are marked with a *. (None is peculiar to this locality.)

List No. 10.

1. *Fusconaia subrotunda* (Lea)
*2. *Crenodonta plicata undulata* (Barn.)
3. *Quadrula tuberculata* (Barn.)
4. *Quadrula metanevra wardi* (Lea)
5. *Quadrula cylindrica* (Say)
6. *Rotundaria tuberculata* (Raf.)
*7. *Pleurobema obliquum coccineum* (Conr.)
*8. *Pleurobema clava* (Lam.)
*9. *Elliptio dilatatus* (Raf.)
*10. *Symphynota costata* (Raf.)
11. *Hemilastena ambigua* (Say)

*12. *Anodonta grandis* Say
*13. *Alasmidonta marginata* (Say)
*14. *Strophitus edentulus* (Say)
15. *Ptychobranchus phaseolus* (Hildr.)
*16. *Obovaria circulus lens* (Lea)
*17. *Eurynia fabalis* (Lea)
*18. *Eurynia iris* (Lea)
*19. *Lampsilis luteola* (Lam.)
*20. *Lampsilis ovata ventricosa* (Barn.)
*21. *Lampsilis multiradiata* (Lea)
22. *Truncilla triquetra* Raf.
23. *Truncilla perplexa rangiana* (Lea)

This is a fauna very similar to that farther below, but somewhat depauperated. It is remarkable that this fauna goes far up, and that there are yet 14 species at the uppermost locality (Weston), where the river is merely a creek. Also here the rule holds good, that the typical Ohio fauna decreases in richness in an upstream direction, and that this decrease is gradual, not sudden.

In sharp contrast to this are the eastern tributaries of the Monongahela, which come down from the mountains. The first of them is the *Youghiogheny River.* The fauna of the lower parts of this river is entirely lost on account of pollution. Between Connelsville and Confluence, Fayette Co., Pa., the river runs through a canyon, is very rough, forming falls (largest at Ohiopyle). Above Confluence it is less rapid, and flows in a broad valley, offering conditions favorable to Najades; but only a single species is found here:

Strophitus edentulus (Say).

The next of the mountain streams is *Cheat River.* Also this river runs through a long canyon, and above this canyon there are no Najades in it.[3] But below the canyon the fauna is rich. In the following list, the species marked * are found also at Mont Chateau,

[3] I collected above Parsons, Tucker Co., W. Va., in *Shavers Fork.* Below Parsons the river is badly polluted, and also *Dry Fork* is polluted through *Blackwater River.* I have been told that there used to be some shells in the Cheat, below Parsons, but we have no means of ascertaining what species they were.

W. Va., immediately below the canyon, the others are from Cheat Haven in Pennsylvania, about eight miles farther below.

List No. 11.

1. *Fusconaia subrotunda* (Lea)
2. *Crenodonta plicata undulata* (Barn.)
3. *Quadrula pustulosa* (Lea)
4. *Rotundaria tuberculata* (Raf.)
5. *Pleurobema clava* (Lam.)

*6. *Elliptio dilatatus* (Raf.)
*7. *Symphynota costata* (Raf.)
*8. *Alasmidonta marginata* (Say)
*9. *Strophitus edentulus* (Say)
*10. *Ptychobranchus phaseolus* (Hildr.)

11. *Nephronaias ligamentina* (Lam.)
12. *Eurynia iris* (Lea)

*13. *Eurynia recta* (Lam.)
*14. *Lampsilis ovata ventricosa* (Barn.)
*15. *Lampsilis multiradiata* (Lea)

The eight species found near Mont Chateau are not in the main channel of the river, but in small side branches, which are more or less protected. In the main channel the bottom consists of large boulders and rocks, not firmly packed, but loose and easily movable, chiefly at flood stage. Moving and shifting bottom prevents permanent settlement of Najades. At Cheat Haven conditions are more favorable, and here we have a rich fauna, agreeing well with that of the lower Monongahela, but of course somewhat depauperated corresponding to the smaller size of the river.

Tygart Valley River, which joins West Fork River at Fairmont, to form the Monongahela, has the same character as the Cheat. There is a more slowly running upper part, above Elkins, Randolph Co., W. Va., a rather long canyon, down to Grafton, and a less rough portion below this. In the canyon a tributary flows into it, *Buckhannon River,* which again is running more slowly in its upper part.

In the lower Tygart, the fauna has been destroyed by pollution. The upper part, above Elkins, contains only two species:

Symphynota costata (Raf.)
Strophitus edentulus (Say)

The upper part of the Buckhannon drainage has one species:

Strophitus edentulus (Say)

I found this not in the river itself, which is dammed and has slack water, but in a small tributary, *French Creek,* at Hampton, Upshur Co., W. Va.

Thus, in these mountain streams tributary to the upper Monongahela, we meet with conditions entirely different from those in the upper Allegheny and its tributaries: the rich Ohio fauna, only slightly depauperated, goes up to a certain point, up to the lower end of a canyon, which represents an extremely rough part of these rivers. This is best observed in the case of the Cheat (list no. 11), while in the others pollution has destroyed the original conditions. But we may easily imagine what these were when we look at the fauna of the plateau stream, West Fork River (see list 10). At the lower end of the canyon the fauna suddenly stops, and above the canyon, in the high valleys, where the rivers are more quiet, very few species, one or two, are found, if such are present at all. It should be noted that one species, *Strophitus edentulus,* is found in all three rivers, which have shells, but that *Symphynota costata* is only in the Tygart.

Thus the canyon apparently forms here a natural barrier.

V. Fauna of the Kanawha River.

Farther to the south we have the Kanawha drainage in West Virginia. The fauna of the Kanawha itself is unknown, for this river is much polluted, and has been transformed into a series of pools by dams, conditions unfavorable for Najad-life.

However, there are two tributaries in the plateau-region, which contain shells. The first is *Elk River.* Here I collected repeatedly and was able to secure the following species. Those marked * are from the uppermost station, at Sutton, Braxton Co., W. Va.

List No. 12.

*1. *Fusconaia subrotunda leucogona* Ort.
*2. *Fusconaia undata trigona* (Lea)
*3. *Crenodonta plicata undulata* (Barn.)
4. *Quadrula pustulosa* (Lea)
*5. *Quadrula tuberculata* (Barn.)
6. *Rotundaria tuberculata* (Raf.)
*7. *Pleurobema clava* (Lam.)
8. *Elliptio crassidens* (Lam.)
*9. *Elliptio dilatatus* (Raf.)
*10. *Symphynota costata* (Raf.)
11. *Alasmidonta marginata* (Say)
*12. *Strophitus edentulus* (Say)
*13. *Ptychobranchus phaseolus* (Hildr.)
*14. *Obovaria circulus* (Lea)
15. *Nephronaias ligamentina* (Lam.)
*16. *Proptera alata* (Say)
17. *Eurynia fabalis* (Lea)
*18. *Eurynia iris* (Lea)
19. *Eurynia recta* (Lam.)
20. *Lampsilis ovata* (Say)
*21. *Lampsilis ovata ventricosa* (Barn.)
*22. *Lampsilis multiradiata* (Lea)

This fauna is of typical upper Ohio character (compare lists 2 and 3). With one exception (*Fusconaia subrotunda leucogona*) every form is also found in western Pennsylvania, and this one is only the local representative of *Fusconaia subrotunda.* Yet this fauna has a somewhat peculiar "facies" in so far as it contains several forms, which elsewhere prefer larger rivers (*Fusconaia undata trigona, Elliptio crassidens, Obovaria circulus, Proptera alata*).

In addition I collected some shells in *Coal River,* at Sproul, Kanawha Co., W. Va.

1. *Fusconaia undata rubiginosa* (Lea)
2. *Crenodonta plicata undulata* (Barn.)

3. *Strophitus edentulus* (Say)
4. *Obovaria circulus lens* (Lea)
5. *Lampsilis luteola* (Lam.)
6. *Lampsilis multiradiata* (Lea)

And the Carnegie Museum possesses, from *Little Coal River,* from the Hartman collection:

7. *Quadrula pustulosa* (Lea)
8. *Quadrula metanevra wardi* (Lea)
9. *Pleurobema obliquum coccineum* (Conr.)

This would add 5 forms (nos. 1, 4, 5, 8, 9), so that 27 forms are known from the lower Kanawha drainage, which are practically all typical upper Ohio forms.

Going up the Kanawha, we find that this river, as *New River,* comes through a canyon out of the mountains. This canyon is extremely rough, containing several falls (Kanawha falls at lower end of canyon, and New Richmond falls, eight miles below Hinton. Good photographs of New River scenery have been published by Campbell and Mendenhall, 1896). In the region of Hinton, Summers Co., W. Va., the river is somewhat less rough. Here I collected, at the confluence of *New River* and *Greenbrier River,* the following species:

List No. 13.

1. *Quadrula tuberculata* (Barn.)
2. *Rotundaria tuberculata* (Raf.)
3. *Elliptio dilatatus* (Raf.)
4. *Symphynota tappaniana* (Lea)

To these, probably, *Alasmidonta marginata* (Say) should be added, for it is found farther up in the New River drainage, and thus we would have five species here, four of which are found in the lower Kanawha drainage, while one (*Symphynota tappaniana*) is entirely new, and found nowhere else in the whole upper Ohio drainage. In fact, this is a species known hitherto only from the Atlantic watershed.

Farther up I collected in the *Greenbrier River* at Ronceverte, Greenbrier Co., W. Va.; in *New River* at Pearisburg, Giles Co., Va.;

and in *Reed Creek,* Wytheville, Wythe Co., Va. Three species only are present here:

List No. 14.

1. *Elliptio dilatatus* (Raf.)
2. *Symphynota tappaniana* (Lea)
3. *Alasmidonta marginata* (Say)

At Pearisburg I did not find no. 3, but at the other localities all three were present. In addition, *Elliptio dilatatus* has been reported by Call ('85, p. 30) from *Bluestone River* (tributary to New River, emptying into it just above Hinton).[4]

These conditions correspond closely to what we have observed in the case of the mountain streams tributary to the Monongahela. There is a rough part in the river in the shape of a canyon. Below the canyon the fauna is rich, above it is extremely poor. In the present case two species (*Quadrula tuberculata* and *Rotundaria tuberculata*) have gone up through the lower part of the canyon, but they were unable to go farther, and the uppermost parts of the New River system, where conditions undoubtedly are favorable for Najades, contain only three species, two of which belong to the Ohio fauna, *while the third is a complete stranger.* With the exception of this case, which will be further discussed below, the whole Kanawha fauna, including that of New River, is undistinguishable from the general upper Ohio fauna. But it should be noted that the species found in the headwaters of the Kanawha are different from those found in the headwaters of the mountain tributaries of the Monongahela.

VI. Big Sandy and Licking Rivers.

South of the headwaters of New River, in the Greater Allegheny Valley, we strike the headwaters of the Tennessee drainage, Holston,

[4] Bluestone River is now badly polluted. I have seen it in its upper part, at Rock, Mercer Co., W. Va. Call (*ibid.,* p. 55) already gives *Rotundaria tuberculata* (as *Unio verrucosus* Barn.) from New River, *Virginia*: but according to my investigations, this is only in the New River in *West Virginia* (at Hinton). Call also says Bluestone River, Virginia, but only the extreme headwaters are in Virginia, the rest in West Virginia.

Clinch and Powell Rivers. However, to the west of these, on the Allegheny Plateau, there are other rivers, tributary to the Ohio, the fauna of which was hitherto entirely unknown. Since a quite different fauna turns up in the Tennessee, it would be surely interesting to know something about these intermediate western rivers, and for this reason I made several trips into this region, and was able to collect the following data, first for the *Levisa Fork of Big Sandy River,* at Prestonsburg, Floyd Co., Ky.

1. *Fusconaia subrotunda* (Lea)
2. *Crenodonta plicata undulata* (Barn.)
3. *Quadrula pustulosa* (Lea)
4. *Quadrula tuberculata* (Barn.)
5. *Elliptio crassidens* (Lam.)
6. *Symphynota costata* (Raf.)
7. *Obovaria circulus lens* (Lea)
8. *Nephronaias ligamentina* (Lam.)
9. *Amygdalonaias elegans* (Lea)
10. *Proptera alata* (Say)
11. *Eurynia recta* (Lam.)
12. *Lampsilis ovata ventricosa* (Barn.)

In the *Licking River,* at Farmer, Rowan Co., Ky., I found:

1. *Crenodonta plicata undulata* (Barn.)
2. *Quadrula pustulosa* (Lea)
3. *Quadrula tuberculata* (Barn.)
4. *Pleurobema obliquum coccineum* (Conr.)
5. *Elliptio dilatatus* (Raf.)
6. *Symphynota costata* (Raf.)
7. *Anodonta grandis* Say
8. *Strophitus edentulus* (Say)
9. *Ptychobranchus phaseolus* (Hildr.)
10. *Obovaria circulus lens* (Lea)
11. *Nephronaias ligamentina* (Lam.)
12. *Proptera alata* (Say)
13. *Lampsilis luteola* (Lam.)
14. *Lampsilis ovata ventricosa* (Barn.)

In a tributary of the Licking, *Fleming Creek* at Pleasant Valley, Nicholas Co., Ky., I found, aside from *Anodonta grandis* and *Lampsilis luteola:*

15. *Anodontoides ferussacianus* (Lea)

Although these two lists give by no means the complete faunas of these rivers, they show clearly that they are practically identical with the upper Ohio drainage in West Virginia and western Pennsylvania. All these species have occurred in our previous lists, with one exception, the very last one, *Anodontoides ferussacianus*. This is a western and northern species. Of the characteristic Tennessee (and Cumberland) drainage fauna not a trace is seen in these rivers.

It is unknown at present whether there is a point in the upper parts of these rivers, where the fauna stops suddenly in an upstream direction. My chief object in introducing here the faunas of these rivers is to show that they cannot be separated from the general Ohio fauna.

VII. Fauna of Upper Tennessee River.

We come now to the Tennessee River. It is well known that this system contains an extremely rich fauna, with a large number of peculiar types. It is not my object to go into detail here, and I only want to bring out the contrast of this fauna to that of the upper Ohio in general, and especially to that of upper New River. With this in view, I collected (September, 1912) in the uppermost parts of *Holston* and *Clinch Rivers* in Virginia. Of course, my collections are by no means complete, as is clearly shown by a comparison with the list published for Holston River by Lewis ('71), which, however, needs revision. But what I have found is sufficient for the present purpose.

List No. 16.

Middle and *North Fork Holston,* in Smyth Co.
(Those marked * only in Middle Fork.)

1. *Fusconaia* sp.?
2. *Pleurobema* (possibly 2 species)
3. *Pleurobema fassinans* (Lea)

4. *Symphynota costata* (Raf.)
5. *Alasmidonta minor* (Lea)
6. *Alasmidonta fabula* (Lea)
7. *Alasmidonta marginata* (Say)
8. *Strophitus edentulus* (Say)
9. *Ptychobranchus subtentus* (Say)
10. *Nephronaias perdix* (Lea)
*11. *Nephronaias copei* (Lea)
12. *Medionidus conradicus* (Lea)
13. *Eurynia nebulosa* (Conr.)
*14. *Eurynia dispansa* (Lea)
15. *Eurynia vanuxemensis* (Lea)
16. *Lampsilis ovata ventricosa* (Barn.)
17. *Lampsilis multiradiata* (Lea)

Clinch, in Tazewell Co.

1. *Fusconaia bursa-pastoris* (Wright)
2. *Fusconaia* sp.?
3. *Quadrula cylindrica strigillata* (Wright)
4. *Pleurobema* (probably 2 species)
5. *Elliptio dilatatus* (Raf.)
6. *Symphynota holstonia* (Lea)
7. *Symphynota costata* (Raf.)
8. *Alasmidonta minor* (Lea)
9. *Alasmidonta marginata* (Say)
10. *Strophitus edentulus* (Say)
11. *Ptychobranchus subtentus* (Say)
12. *Medionidus conradicus* (Lea)
13. *Eurynia perpurpurea* (Lea)
14. *Eurynia nebulosa* (Conr.)
15. *Eurynia planicostata* (Lea)
16. *Lampsilis ovata ventricosa* (Barn.)
17. *Lampsilis multiradiata* (Lea)
18. *Truncilla haysiana* (Lea)
19. *Truncilla capsaeformis* (Lea)

These are altogether about 26 species, of which only 6 have occurred in our previous lists (*Elliptio dilatatus, Symphynota cos-*

tata, Alasmidonta marginata, Strophitus edentulus, Lampsilis ovata ventricosa, Lampsilis multiradiata). All others (about 20) are not found in the upper Ohio drainage; some have representative forms there (*Fusconaia bursa-pastoris, Quadrula cylindrica strigillata, Eurynia nebulosa, Truncilla capsaeformis*); but others are types, which are not at all represented there (*Pleurobema fassinans, Alasmidonta minor* and *fabula,* the genus *Medionidus, Eurynia perpurpurea* and *vanuxemensis, Truncilla haysiana* are the most important ones).

It should be noted especially that the New River species, *Elliptio dilatatus* and *Alasmidonta marginata,* which are found in the Tennessee drainage, are not represented by identical forms. *Elliptio dilatatus* of upper New River is a dwarf race, while the Clinch type is large and normal. The Clinch and Holston type of *Alasmidonta marginata* is peculiar by its extremely bright color markings.

The contrast between these rivers is thus clearly established, and becomes even more striking, when we consider the fact that in general physiographic characters these rivers are very similar to each other, and further, that the Holston and Clinch, where I collected in them, are much smaller, mere creeks, compared, for instance, with New River at Pearisburg.

Summary of Facts Concerning the Western Fauna.

To express it in a few words, the chief features of the western fauna are: a *uniform fauna* goes from Licking River up through the whole upper Ohio drainage into the headwaters of the Allegheny, but in the mountain streams tributary to the Monongahela and Kanawha *a sudden depauperation is observed and farther above very few species are present.* The fauna of the upper Tennessee is related to the Ohio fauna, but has *many peculiar elements.* As a whole, the Ohio fauna is to be regarded as a somewhat depauperated Tennessee fauna; this is not so evident from the lists given above, but is a well-known fact, for which we do not need to furnish here particular proof.

B. ATLANTIC SIDE.

Besides the writer's own investigations, the following publications have been used for compilation of the faunistic lists:

For Delaware, Susquehanna, and Potomac rivers: Gabb, 1861; Hartman and Michener, 1874; Pilsbry, 1894; Schick, 1895; Caffrey, 1911.

For James River: Conrad, 1846.

Since the Atlantic side does not form a single drainage system, but consists of a number of rivers running independently to the sea, we must discuss these rivers separately.

I. The Fauna of the Delaware River.

This is the most northern system in the region discussed here. The following Najades are known to exist here:

List No. 17.

1. *Margaritana margaritifera* (L.)
2. *Elliptio complanatus* (Dillw.)
3. *Elliptio fisherianus* (Lea)
4. *Symphynota tappaniana* (Lea)
5. *Anodonta cataracta* Say
6. *Anodonta implicata* Say
7. *Alasmidonta heterodon* (Lea)
8. *Alasmidonta undulata* (Say)
9. *Alasmidonta varicosa* (Lam.)
10. *Strophitus undulatus* (Say)
11. *Strophitus edentulus* (Say)
12. *Eurynia nasuta* (Say)
13. *Lampsilis radiata* (Gmel.)
14. *Lampsilis cariosa* (Say)
15. *Lampsilis ochracea* (Say)

It is to be remarked that no. 3, no. 10 and no. 15 are found exclusively in the tidewater region of the lower Delaware and Schuylkill, and that no. 3 is at the best extremely rare (only once reported), and that no. 10 is altogether a doubtful form. No. 1 is very local (uppermost Schuylkill).

All the others go up beyond tidewaters, and are found in the Delaware River or its tributaries on the Piedmont Plateau. The Allegheny Valley and its eastern boundary being obscured in this region, it practically is connected with the Piedmont Plateau. The Delaware River proper extends soon into the Glacial area, but there are tributaries outside of it west (northwest) of the Blue Mountain (Kittatinny Mountain), belonging to *Lehigh River.* The Lehigh itself is polluted; but I have collected in this region the following species (*Princess Cr.* and *Meniolagomeka Cr.,* at Kunkletown and Smith Gap, Monroe Co.; *Mahoning Cr.,* Leheighton, Carbon Co.; and *Lizard Cr.,* Mantz, Schuylkill Co.).

1. *Elliptio complanatus* (Dillw.)
2. *Anodonta cataracta* Say
3. *Alasmidonta heterodon* (Lea)
4. *Alasmidonta undulata* (Say)
5. *Alasmidonta varicosa* (Lam.)
6. *Strophitus edentulus* (Say)

Possibly the list is not quite complete (*Symphynota tappaniana* might be here). But I never found all of these species associated at a single locality, and it should be stated right here that it is a general rule that on the Atlantic side certain species are of rather erratic distribution, being sometimes missing at certain localities for no apparent reasons, while at others they may be abundant.

With the exception of *Margaritana margaritifera,* probably all of the Delaware River species (14) were once found in the lower part of *Schuylkill River.* Although the fauna of this river has been studied for nearly one hundred years, reliable information about the details of the distribution of the shells are not at hand. At the present time this river is so polluted that the fauna is extinct, only in the Schuylkill canal is a rather rich remnant of at least 8 species (nos. 2, 4, 5, 7, 8, 11, 12, 13 of list no. 17). Thus we cannot form an idea of how far the species advanced upstream and shall never know this.

In the headwaters of the *Little Schuylkill River,* in Schuylkill Co., northwest of Blue Mountain, a very peculiar species turns up,

Margaritana margaritifera, and still exists there, and I have collected it repeatedly in 1909 and 1910. But it has become very rare, and is restricted to some small, clear, and cold mountain runs, in which no other Najades are found. This species stands by itself, and, as we shall see below, needs special discussion.

II. The Fauna of the Susquehanna River.

The following is a list of the species, positively known to occur in the Susquehanna drainage:[5]

List No. 18.

1. *Elliptio complanatus* (Dillw.)
2. *Symphynota tappaniana* (Lea)
3. *Anodonta cataracta* Say
4. *Alasmidonta undulata* (Say)
5. *Alasmidonta marginata susquehannae* Ortm.
6. *Alasmidonta varicosa* (Lam.)
7. *Strophitus edentulus* (Say)
8. *Lampsilis radiata* (Gmel.)
9. *Lampsilis cariosa* (Say)

The lower Susquehanna, in Maryland, is unknown. Possibly, the lowland and tidewater species, *Elliptio fisherianus* and *Lampsilis ochracea,* might be found there. And further, *Alasmidonta heterodon* has not been taken in the Susquehanna drainage, although it is present to the north and south of it. Even adding these three species, the fauna of the Susquehanna falls short of that of the Delaware by three species; four seem to be absent (*Margaritana margaritifera, Anodonta implicata, Strophitus undulatus, Eurynia nasuta*), while *Alasmidonta marginata susquehannae* is added. The first two species surely reach their southern boundary in the Delaware drainage, while the doubtful *Strophitus undulatus* seems to be

[5] *Anodontoides ferussacianus* (Lea) has been reported from the headwaters of the Susquehanna in New York state. It is not found in Pennsylvania, and the New York record should be confirmed; but even when correct, this may be neglected, for this species surely does not belong to the original fauna of this system, but is a postglacial immigrant.

local, and *Eurynia nasuta* has been reported farther south on the Coastal Plain (as far as North Carolina by Simpson; from James River by Conrad, '36; from the lower Potomac by Dewey, '56; and Marshall, '95). But these localities should be confirmed, since this species has been frequently confounded with *Elliptio productus* and *fisherianus*. According to Rhoads ('04), it is also in Sussex and Kent Cos., in Delaware.

The Susquehanna drainage extends not only into the Allegheny Valley and into the mountains, but clear through the mountains, and encroaches upon the Allegheny plateau. All of the species mentioned above go up into this region, but two of them have only a limited distribution, and seem to be restricted to the larger rivers. These are *Lampsilis radiata* and *L. cariosa*. Both of them go in the North Branch to the New York state line. In the Juniata is only *L. cariosa* (up to Huntingdon, Huntingdon Co.), and in the West Branch both go up at least to Williamsport, Lycoming Co. In the real headwaters there are only seven species, and they are not always associated at a particular locality (generally there are only from three to six together).

One locality is of special interest: this is *Cush Cushion Creek,* in Greene Twp., Indiana Co. This is the most western point to which the Susquehanna fauna advances, and the following species are here:

1. *Elliptio complanatus* (Dillw.)
2. *Symphynota tappaniana* (Lea)
3. *Alasmidonta varicosa* (Lam.)
4. *Strophitus edentulus* (Say)

Not very far from here, in *Chest Creek,* Patton, Cambria Co., I found:

1. *Elliptio complanatus* (Dillw.)
2. *Symphynota tappaniana* (Lea)
3. *Alasmidonta undulata* (Say)
4. *Strophitus edentulus* (Say)

Also *Anodonta cataracta* Say has been found in this region, in *Beaver Dam Creek,* Flinton, Cambria Co. Thus there would be six

species in this uppermost part of the drainage of West Branch. *Alasmidonta marginata susquehannae* has not been found here.

The seven species of the upper Susquehanna drainage are the same as those of the Delaware, with the exceptions that in the former *Margaritana* and *Alasmidonta heterodon* are missing, while in their place *Symphynota tappaniana* and *Alasmidonta marginata susquehannae* turn up. Thus there are five species common to both drainages.

Further investigations may change this slightly. But this seems to be assured, that although similar faunas exist in both rivers, the Susquehanna falls short by several species of the Delaware, and that the lack is made good only in part by the presence of a local form, *Alasmidonta marginata susquehannae.*

III. The Fauna of the Potomac River.

The following species are positively known to exist in the Potomac drainage:

List No. 19.

1. *Elliptio complanatus* (Dillw.)
2. *Elliptio productus* (Conr.)
3. *Symphynota tappaniana* (Lea)
4. *Anodonta cataracta* Say
5. *Alasmidonta undulata* (Say)
6. *Alasmidonta varicosa* (Lam.)
7. *Strophitus edentulus* (Say)
8. *Lampsilis radiata* (Gmel.)
9. *Lampsilis ovata cohongoronta* Ortm.
10. *Lampsilis cariosa* (Say)
11. *Lampsilis ochracea* (Say)

In addition, there might be, in the lower Potomac, *Elliptio fisherianus* (Lea) and *Eurynia nasuta* (Say); these have been frequently confounded, but forms like them are positively known to occur in the Potomac at Washington. Possibly both of them are there. Further, there might be, in the tributaries on the Piedmont Plateau, *Alasmidonta heterodon* (Lea), which is found both to the north and south of the Potomac drainage.

No. 9, *Lampsilis ovata cohongoronta,* should be disregarded, and dropped from the list of the original fauna of the Potomac, for it probably is a modern introduction from the west (Ortmann, 1912*b*).

Thus, including the doubtful forms, there would be 13 species belonging to the Potomac drainage. This is two less than in the Delaware; while three of the latter are missing here (*Margaritana margaritifera, Anodonta implicata, Strophitus undulatus*), one other is added, *Elliptio productus.* This latter case is important, because we positively know that this species is a southern form, which reaches its most northern range in the Potomac.

Aside from *Elliptio fisherianus* and *Eurynia nasuta,* which, when present, are found only in the lower Potomac, three others, *Lampsilis radiata, cariosa,* and *ochracea,* are restricted to the lower parts of the drainage, below the gap in the Blue Ridge at Harper's Ferry. Above and to the west of this point, that is to say, in the Allegheny Valley and the Allegheny Mountains, only the following species are present (of course, disregarding the introduced no. 9):

1. *Elliptio complanatus* (Dillw.)
2. *Elliptio productus* (Conr.)
3. *Symphynota tappaniana* (Lea)
4. *Anodonta cataracta* Say
5. *Alasmidonta undulata* (Say)
6. *Alasmidonta varicosa* (Lam.)
7. *Strophitus edentulus* (Say)

Also here, seven species ascend into the headwaters, and among them there are again the same five (*Elliptio complanatus, Anodonta cataracta, Alasmidonta undulata, Alasmidonta varicosa, Strophitus edentulus*) which we have seen to be common to the headwaters of the Delaware and Susquehanna. An additional one, *Symphynota tappaniana,* is also found in the Susquehanna, while *Elliptio productus* is a new element in this fauna.

I do not think it necessary to give further particulars. But again it should be noted, that the distribution of these species is rather erratic, and that they generally are not all found associated. *Elliptio productus* has not been found yet in the region of the Alle-

gheny Valley (Antietam and Conodoguinet creeks in Maryland and Pennsylvania, Shenandoah River in the Virginias), but it is rather frequent in the Potomac and its tributaries in West Virginia, Maryland and Pennsylvania in the region of the Allegheny Mountains.

IV. The Fauna of Rappahannock River.

The *Rappahannock* is a Piedmont Plateau stream, and is entirely east of the Blue Ridge. I collected near the headwaters about Remington, Fauquier Co., and Culpepper and Rapidan, Culpepper Co., Va. The following is the list:

List No. 20.

1. *Elliptio complanatus* (Dillw.)
2. *Elliptio productus* (Conr.)
3. *Elliptio lanceolatus* (Lea)
4. *Symphynota tappaniana* (Lea)
5. *Alasmidonta heterodon* (Lea)
6. *Alasmidonta undulata* (Say)
7. *Strophitus edentulus* (Say)

I give this list only for comparison; probably it is not quite complete. The interesting points are, that *Alasmidonta heterodon* turns up here again, and that there is here a new, southern form, which does not go farther north (*Elliptio lanceolatus*).

V. The Fauna of the Upper James River.

I did not do any collecting in James River east of Blue Ridge, and although a few records are at hand from the lower James, it is impossible to give a complete list. West of Blue Ridge, the fauna of *North River* (called *Calf Pasture River* in its upper part) has been studied many years ago by Conrad (1846). I place his list by the side of the forms collected by myself in this region:

List No. 21.

Conrad's list:	Species collected by myself:
Unio subplanus Conr.	= 1. *Lexingtonia subplana* (Conr.)
Unio purpureus Say	= 2. *Elliptio complanatus* (Dillw.)

Unio lanceolatus Lea, probably	= 3. *Elliptio productus* (Conr.)
	4. *Symphynota tappaniana* (Lea)
Unio collinus Conr.	= 5. *Alasmidonta collina* (Conr.)
Alasmodon undulata Say	= 6. *Alasmidonta undulata* (Say)
	7. *Strophitus edentulus* (Say)
Unio constrictus Conr.	= 8. *Eurynia constricta* (Conr.)
Alasmodon marginata Say	
Anodon cataracta Say	
Anodon marginata? Say	

I did not find *U. lanceolatus,* but in its place *Ell. productus* is very abundant, so that, I believe, Conrad confused these two species. *Anodonta marginata* is given by him as doubtful, and we may rest assured that this (northern) species is not found here. But it is quite possible that *Alasmodon marginata* (now *Alasmidonta varicosa*) and *Anodonta cataracta* are here, and I do not hesitate to add these to my list: My list has two species, not mentioned by Conrad. Thus we would have ten species in the upper James drainage. The five species common to the headwaters of the more northern Atlantic streams are again here, there is one species (*Symphynota tappaniana*) known from upper Susquehanna and Potomac, one species (*Ell. productus*), known from upper Potomac, and three species, which turn up here for the first time:

Lexingtonia subplana
Alasmidonta collina
Eurynia constricta

These additional elements are undoubtedly more southern types, which reach here their most northern station.

VI. The Fauna of the Upper Roanoke River.

Only the uppermost *Roanoke* is known to me. It drains a relatively small portion of the Allegheny Valley, chiefly in Roanoke and Montgomery Cos., Va., and has the following, poor fauna:

List No. 22.

1. *Elliptio complanatus* (Dillw.)
2. *Strophitus edentulus* (Say)
3. *Eurynia constricta* (Conr.)

These species are all found in the upper James, and one of them (no. 3) clearly shows the affinity with that system. This is undoubtedly a depauperated fauna, corresponding to the small size of the streams. Possibly the record is not complete. Below Roanoke, the river is polluted, but east of the Blue Ridge there are surely additional species in this system.

SUMMARY OF FACTS CONCERNING THE EASTERN FAUNA.

Full list of all species known to exist on the Atlantic slope (in the region investigated):

List No. 23.

1. *Margaritana margaritifera* (L.)
2. *Lexingtonia subplana* (Conr.)
3. *Elliptio complanatus* (Dillw.)
4. *Elliptio fisherianus* (Lea)
5. *Elliptio productus* (Conr.)
6. *Elliptio lanceolatus* (Lea)
7. *Symphynota tappaniana* (Lea)
8. *Anodonta cataracta* Say
9. *Anodonta implicata* Say
10. *Alasmidonta collina* (Conr.)
11. *Alasmidonta heterodon* (Lea)
12. *Alasmidonta undulata* (Say)
13. *Alasmidonta marginata susquehannae* (Ortm.)
14. *Alasmidonta varicosa* (Lam.)
15. *Strophitus undulatus* (Say)
16. *Strophitus edentulus* (Say)
17. *Eurynia constricta* (Conr.)
18. *Eurynia nasuta* (Say)
19. *Lampsilis radiata* (Gmel.)
20. *Lampsilis cariosa* (Say)
21. *Lampsilis ochracea* (Say)

Lampsilis ovata cohongoronta Ortm. has been dropped as not indigenous on the Atlantic slope.

The following facts are observed:

1. Probably seven species of these have a rather general distribution. In five of them this is perfectly clear (nos. 3, 8, 12, 14, 16), but probably also nos. 7 and 11 fall under these; they only may have been overlooked in certain regions.

2. There are six forms, which apparently have a more northern range, disappearing toward the south, nos. 1, 9, 18, 19, 20, 21. The last four have the peculiarity in common that toward the south they become more or less restricted to the coastal plain.

3. On the other hand, there are six forms, which have their center more toward the south and disappear toward the north. These are the nos. 2, 4, 5, 6, 10, and 17.

4. Of the two remaining forms, no. 13 is a local form of the Susquehanna drainage, while no. 15 is altogether doubtful, but may be a local (tidewater) form of no. 16.

Compared with the western fauna of 47 species (list no. 1), the Atlantic fauna is decidedly poor (less than half the number of species). But in the Ohio we notice a general and marked decrease of species in the headwaters, so that there are only fourteen species in the headwaters of the Allegheny River. In the eastern drainage systems, there is also a slight decrease toward the headwater, but this is much less in proportion, and in the mountain region we have yet thirteen species (nos. 1, 2, 3, 5, 7, 8, 10, 11, 12, 13, 14, 16, 17). Thus we may say, that, disregarding a few species restricted to the lowlands and the larger rivers, *the fauna of the Atlantic streams remains, in each river system, rather uniform up to the headwaters,* decreasing hardly in the number of species.

Further, in the region of the headwaters of the Monongahela and Kanawha, the conditions are actually reversed. Here only very few species (not more than three) are found in the western streams, while the eastern streams (Potomac, James) have decidedly more, the James, for instance, at least eight, possibly ten. *Thus the Atlantic fauna is here richer than the western.*

But the Tennessee fauna (list no. 16) again holds its own, and the Atlantic fauna falls by far short of it.

Chapter 2.

Systematic Affinities of the Najades of the Interior Basin and of the Atlantic Slope.

In order to understand the mutual relations of the western and eastern faunas, which, as we have seen, are at present rather sharply distinguished, it is necessary to consider the systematic affinities of the forms belonging to either.

Up to a comparatively recent time the natural system of the Najades was extremely obscure. However, the great synopsis of Simpson (1900*a*) has paved the way for a proper understanding of the relationship of our Najades, and the more recent papers of the present writer (chiefly 1912*a*) have furnished what is believed to be the natural system, expressing, as far as possible, the genetic affinities within this group.

Using this system as a guide, the following remarks are to be made:

I. The general fauna of the upper Ohio drainage (list no. 1, p. 291) contains no less than seventeen genera, which are not found on the Atlantic side, namely:

Fusconaia	*Hemilastena*	*Amygdalonaias*
Crenodonta	*Ptychobranchus*	*Plagiola*
Quadrula	*Obliquaria*	*Paraptera*
Rotundaria	*Cyprogenia*	*Proptera*
Plethobasus	*Obovaria*	*Truncilla*
Pleurobema	*Nephronaias*	

This is entirely sufficient to show the tremendous difference between the two faunas, and demonstrates clearly that *the Allegheny Mountains formed an important barrier to the eastward distribution of the bulk of the western fauna.* No further discussion of this is required.

II. The fauna of the headwaters of the Allegheny River (combined lists 6, 7, 8, 9, p. 301) contains five species (out of fourteen) which are typically western and belong to genera just mentioned:

Fusconaia undata rubiginosa
Pleurobema obliquum coccineum
Pleurobema clava
Ptychobranchus phaseolus
Obovaria circulus lens

Another one, *Symphynota costata,* should be added, since, although the genus is found in the east, the subgenera are different (*Lasmigona* and *Symphynota*).

This shows that although a number of the typical western genera have gone way up into the headwaters, *they have not been able to cross the divide.*

III. On the Atlantic side (see list no. 23) we have two genera (*Margaritana* and *Lexingtonia*), which are not found in the interior basin. *Margaritana* has, indeed, a related form (*Cumberlandia monodonta* (Say)) in the Tennessee and Ohio drainage, but there is probably no direct genetic connection between them, and the history of *Margaritana,* as will be seen below, *is a case by itself.*

IV. *Lexingtonia* is possibly related to and descended from certain interior basin forms (such as *Fusconaia* and *Pleurobema*), but the relationship is remote, and for all practical purposes we may class it with the cases to be mentioned presently. These are the following forms (of list no. 23): nos. 3, 4, 5, 6 (the four species of *Elliptio*), and nos. 10, 11, 12 (*Alasmidonta collina, heterodon, undulata*). All these are forms of the respective genera, which have *no closely allied or representative forms on the western side,* although the genera are represented there.

Attention should be called to the fact that *Lexingtonia,* three species of *Elliptio* (*fisherianus, productus, lanceolatus*) and *Alasmidonta collina* undoubtedly belong to the *southern element* in the Atlantic fauna, and that their distribution northward is limited. However, it is also probable that *Elliptio complanatus, Alasmidonta heterodon* and *undulata* belong to the same class. The first and third are undoubtedly southern in their affinities, and allied species are frequent upon the southern portion of the Atlantic slope (in the Carolinas and Georgia). This is not so clear in the case of *Alasmidonta heterodon.* Here it has the appearance, as if the dis-

tribution might be more northern, but this may be due to defective knowledge of the facts.

V. Another group of Atlantic species *has closely allied species in the interior basin.* No. 17 of the list, *Eurynia (Micromya) constricta,* has a representative form in the upper Tennessee drainage (*Eurynia (Micromya) vanuxemensis*). Six others (nos. 8, 9, 14, 19, 20, 21) have closely related, indeed representative forms, in the upper Ohio drainage. The relation is as follows:

no. 8 and 9, *Anodonta cataracta* and *implicata,* represent the western *Anodonta grandis.*

no. 14, *Alasmidonta varicosa,* represents the western *Alasmidonta marginata.*

no. 19, *Lampsilis radiata,* represents the western *Lampsilis luteola.*

no. 20 and 21, *Lampsilis cariosa* and *ochracea,* represent the western *Lampsilis ovata ventricosa* (and its allied forms).

It should be noted that just these Atlantic forms are preëminently those which have a more northern range upon the Atlantic side.

VI. Finally, there are four species on the Atlantic side, *which are specifically identical with western forms.* Particulars are as follows:

no. 13, *Alasmidonta marginata susquehannae,* is a local form of the Susquehanna drainage, closely resembling the widely distributed western *Alasmidonta marginata.*

no. 7, *Symphynota tappaniana,* is represented on either side by an absolutely identical form. But here the distribution is rather general on the eastern side and local on the western (New River).

no. 16, *Strophitus edentulus,* is absolutely identical on either side, and also widely distributed, east as well as west. But it should be noted that it is apparently absent in New River.

no. 18, *Eurynia nasuta.* Here we see that the identical species is on the Atlantic side and in Lake Erie basin, but *not* in the upper Ohio drainage.

We see at once that these cases apparently are not subject to the same laws, and further below they shall be treated each by itself.

There remains yet one of the Atlantic forms, no. 15, *Strophitus*

undulatus. We must dismiss this for the present, for we do not know much about its taxonomic standing and its distribution. This may be nothing but a local form of *Strophitus edentulus*, and then it would have to the latter the same relation as *Lampsilis ochracea* has to *L. cariosa* (the former is the tidewater form of the latter).

As a whole, *the Atlantic fauna should be regarded as an offshoot of the fauna of the interior basin*, with the exception of *Margaritana margaritifera*. It does not possess any very strongly marked types of its own, but all may be traced back to western types. However, there are different elements on the Atlantic slope, which apparently reached their present range by different ways, and probably at different times. The greatest independence is shown among those which are found in the southern section of the Atlantic slope, and *there is an indication of the development of a secondary center of dispersal in this region*, producing a few characteristic types, more remote in their affinities from the forms of the interior basin. The other forms are generally more or less closely connected with western species, in fact, clearly are representative forms of them.

Chapter 3.

Distributional Facts in other Freshwater Animals.

Before we advance further in our attempt to study the mutual relations of the eastern and western freshwater faunas, it is well to compare a few other groups with the Najades, in order to ascertain whether there are parallel cases to those described above.

I. SPHAERIIDÆ.

For the identification of my material I am indebted to V. Sterki. Although I have collected a great many *Sphæriidæ* from the streams of Pennsylvania, West Virginia, and Virginia, my collections are by no means complete. Nevertheless, as far as they go, they serve to confirm the well-known fact, that with regard to these small shells, *the Alleghenian divide does not form an important faunistic boundary*. Thus the *Sphæriidæ* distinctly differ from the Najades, and undoubtedly must have been subject to other laws.

It is not necessary to give a detailed account of the single species; it suffices to enumerate those species which I have before me from both sides of the mountains:

Sphærium sulcatum (Lam.)
Sphærium solidulum (Pr.)
Sphærium stamineum (Conr.)
Sphærium striatinum (Lam.)
Musculium transversum (Say)
Musculium truncatum (Linsl.)
Pisidium virginicum (Gmel.)
Pisidium compressum Pr.

Of course, these examples will become more numerous when more exhausting studies have been made.

Altogether, we may safely assume that it is a general rule among this group, that the distribution is not influenced by the Alleghenian divide. As we have seen above, this condition is extremely rare among the Najades. In the present case, the distribution of the *Sphæriidæ* seems to have been formed under the influence of one great general factor, which probably is the faculty of these shells to cross over divides, presumably by being transported. It is very pertinent to bring this out here most emphatically, because, as we have seen, this factor has had very little or no effect among the Najades, as is shown by the entirely different character of their distribution.

II. GASTROPODA, FAMILY: PLEUROCERIDÆ.

The identifications have been kindly furnished by A. A. Hinkley. I have a rather satisfactory material of this family, although the records are not as complete and exhausting as in the Najades.

The whole character of the distribution of these freshwater snails is like that of the Najades, and, consequently, it is indicated that no exceptional means of dispersal (transport) have played a part. The range of the species follows rather closely the river systems, and *the effect of the Alleghenian divide as a barrier is quite evident.* Two facts, however, are to be regretted, first, that in the region

investigated the number of species is not very great, and second, that the natural affinities within this family are yet entirely obscure. Nevertheless, some interesting points are easily observed, as will be seen from the following account.

A. THE UPPER OHIO DRAINAGE in western Pennsylvania and West Virginia has the following species:

1. *Pleurocera canaliculatum* (Say)
2. *Pleurocera altipetum* Anth.
3. *Goniobasis livescens* (Mke.)
   (incl. var. *depygis* (Say))
4. *Goniobasis translucens* Anth.
5. *Anculosa dilatata* (Conr.)

It is to be remarked that the two Pleuroceras are restricted to the larger rivers; no. 1 is in the Ohio proper at and below Pittsburgh, and has also been found as far up as the lower Youghiogheny in Allegheny Co., Pa.; while no. 2 is in the middle Allegheny up to Venango and Warren Cos. No *Pleuroceras* have ever been found in any of the smaller streams.

Goniobasis livescens is in the Beaver drainage, and in that of French Creek of the Allegheny (also in Lake Erie), and it appears as if this species should be classed with those Najades which have been mentioned (on p. 291, footnote 2) to be peculiar to those drainages. The *Goniobasis*-species of the Allegheny River, beginning in the Ohio River below Pittsburgh, and going up through Armstrong, Venango, Forest to Warren Co., is, according to Hinkley, *G. translucens,* and this species is also abundant in the drainages of Beaver River and French Creek.

Except in the lower Youghiogheny, where (many years ago) *Pleurocera canaliculatum* has been found, no species of *Pleurocera* or *Goniobasis* are known from the whole Monongahela drainage. I have no doubt that some existed once at least in the lower Monongahela, but the pollution of the waters apparently has exterminated them, and no records have been preserved. The upper Youghiogheny, where the water is clear, is entirely without *Pleuroceridæ,* and this is positively established, for a search has been made for them.

This is a fact which should be emphasized, for in the headwaters of the Monongahela, *Anculosa dilatata* turns up. This is found in the lower part of the Cheat at Cheat Haven, Fayette Co., Pa., and goes up through the canyon into the headwaters (Shavers Fork, Parsons, Tucker Co., W. Va.); it is also in Tygart Valley River, at Elkins, Randolph Co., W. Va., and even in the plateau stream, West Fork River, at Lynch Mines, Harrison Co., W. Va.

No *Anculosas* are found in the rest of the upper Ohio drainage in western Pennsylvania.

Farther south in West Virginia our knowledge probably is fragmentary. In the *Kanawha drainage,* no *Pleuroceridæ* are known to me, except *Pleurocera validum* Anth. in Elk River; and New River and Greenbrier rivers, at least from Hinton upward, contain *Anculosa dilatata* (Conr.). The latter is exceedingly abundant in this region.

In the *Big Sandy,* at Prestonsburg, Floyd Co., Ky., I collected *Pleurocera unciale* Hald., a species which is also found in Clinch River. *Licking River* at Farmer, Rowan Co., Ky., has *Pleurocera cylindraceum* Lea.

It appears that there is a certain correlation in the distribution of the *Pleuroceridæ* and the *Najades* of the upper Ohio drainage, at least as far as it concerns the genera *Pleurocera* and *Goniobasis.* It is well known that the greatest variety of forms is found in the lower Ohio and its tributaries, and it is suggested that this fauna has migrated upstream, and that there is a general decrease in the number of species in an upstream direction. *But the different tributaries of the upper Ohio seem to have received or have developed different species.* In addition, most of the species do not go very far into the headwaters, and the smaller streams generally do not contain *Pleuroceridæ,* or only rarely so.[6]

One very remarkable fact is to be noted. In the headwaters of the Monongahela, excluding the Youghiogheny, and also in the headwaters of the Kanawha (New and Greenbrier rivers), *Anculosa*

[6] This, however, is different in the Beaver drainage, where species of *Goniobasis* are found in small creeks. But the characteristic species, *G. livescens,* probably did not come up the Ohio, but came "across country" from the West.

is the only genus found, and it is represented in all these streams by one and the same species, A. dilatata. This genus is not found anywhere else in the whole upper Ohio drainage in West Virginia and Pennsylvania, but it is represented on the Atlantic side by a closely allied and widely distributed species. It is perfectly clear that this case does not submit to the same laws which governed the Najad fauna and the other *Pleuroceridæ* of this region. Further particulars will be given below.

As regards the *upper Tennessee* fauna (Clinch and Holston rivers), we have here again a rich development of *Pleuroceridæ,* as is well known. I do not think that my collections represent this fauna fully, but I have collected the following species:

1. *Io fluvialis* (Say) (Holston and Clinch)
2. *Pleurocera estabrooki* (Lea) (Holston)
3. *Pleurocera knoxense* (Lea) (Holston)
4. *Pleurocera unciale* Hald. (Clinch, also, as we have seen, in Big Sandy.)
5. *Goniobasis simplex* (Say) (Holston and Clinch)
6. *Anculosa gibbosa* Lea (Holston and Clinch)

Io is a type entirely peculiar to this region. Except *Pl. unciale,* which is also in the Big Sandy, the others have no striking relationship to any of the species mentioned above from the upper Ohio. The *Anculosa* may have a somewhat closer genetic relationship with the *Anculosas* farther north, in New River, etc., but morphologically they are distinctly separated.

Thus it is clear that the *Pleurocerid*-fauna of the upper Tennessee undoubtedly corresponds to the Najad-fauna of this region, and probably has had a similar history.

B. Pleuroceridæ of the Atlantic Side.

The genus *Pleurocera* is entirely missing on the Atlantic side. *Goniobasis* is represented by two species:[7] *G. virginica* (Gmel.) and

[7] Additional species are found from North Carolina southward. *G. nickliniana* Lea has been reported (Tryon, '66, p. 31) from Bath Co., Va. (original locality: near Hot Springs, drainage of Jackson River). This species is unknown to me. I collected in Jackson River at Covington, Alleghany Co.,

G. symmetrica Hald. The former is common all over the Delaware, Susquehanna, Potomac and James river drainages, and has been found practically everywhere, possibly with the exception of the smallest streams in the headwaters. This species has no closely allied or representative form in the upper Ohio drainage, but if Tryon's arrangement of the species (1866, p. 39 f.) is natural, related forms are found in Tennessee and Alabama. It is unknown how far this species ranges southward, but according to our present knowledge, it seems that it belongs rather to that group of fresh-water forms, *which point in their affinities to a center lying on the southern Atlantic slope.*

Specimens of a *Goniobasis* collected by myself in Mason Creek, Salem, and Tinker Creek, Roanoke, Roanoke Co., Va. (Roanoke drainage) have been identified by Hinkley as *G. symmetrica,* a species reported (Tryon, '66, p. 30) from West Virginia, East Tennessee, South Carolina, North Georgia, and Alabama. But there is much uncertainty about this, and West Virginia seems to be more than doubtful. One fact, however, is sure: this species is not found north of the Roanoke on the Atlantic side. *Thus also this appears as a southern type,* and should be classed with the same group as *G. virginica.*

In addition there is a species of *Anculosa* on the Atlantic side: *A. carinata* (Brug.). This is absent in the Delaware drainage, but extremely abundant in the systems of the Susquehanna, Potomac, James, and Roanoke, and goes far up in the mountain streams. This species is very closely allied to *A. dilatata* of New River and the headwaters of the Monongahela, and undoubtedly stands in closest genetic relationship to it. In fact, these two species are so intimately allied on the one hand and are so polymorphous on the other, that it is extremely hard to distinguish them. It has been mentioned that they also have an allied but more sharply distinguished species in the upper Tennessee (*A. gibbosa*).

There is no doubt that we have to class this case with those of *the very closely allied or identical species of Najades on either side*

less than twenty miles from Hot Springs, but only *Anculosa carinata* was there, in various forms, some of which resemble very much Lea's figure of *G. nickliniana.*

of the divide. The present case most resembles that of *Symphynota tappaniana,* where we have a species found both in New River and on the Atlantic side. The range of the latter is not entirely identical, for it is not found in the Monongahela drainage, and goes, on the Atlantic side, farther north, while *A. carinata* only reaches the Susquehanna in which it goes up to New York state.

III. FAMILY: VIVIPARIDÆ; GENUS: CAMPELOMA RAF.

Also in this group we lack a modern revision of the species, and there is much uncertainty with regard to the geographical distribution. What I have collected in Pennsylvania, West Virginia and Virginia apparently falls under three described species: *Campeloma decisum* (Say), *C. rufum* (Hald.), and *C. ponderosum* (Say), and with the first one I unite as undistinguishable, what has been called *C. integrum* (Say). At any rate, I am not able to distinguish the common form of the upper Ohio drainage in western Pennsylvania and West Virginia from the common form of the Atlantic side (from Delaware to James). The identical form is also in Clinch River.

C. decisum seems to prefer the larger rivers, but it is not absent in the headwaters, and I have it from the mountain region on either side of the divide (Shaver's Fork, upper Tygart system, Greenbrier, uppermost tributaries of Allegheny, and many places in the headwaters of the Potomac and James). Consequently, this would be again a case where *an identical species is found on either side of the divide,* and where this divide does not form a barrier to the distribution.

Of the other two species, *C. rufum* is known to me only from northwestern Pennsylvania, in the Allegheny and its tributaries (French Creek) and in the Beaver and Little Beaver drainage. This looks very much as if it belonged to those forms, *which invaded Pennsylvania from the west,* coming "across country." (After all, this may be only a local form of *C. decisum,* with which it is often found associated.)

I found *C. ponderosum* only in Elk Creek, West Virginia, and farther down in the Ohio (Portsmouth, Scioto Co., Ohio). Here it

is the only *Campeloma* present, and it should be emphasized that in the upper Kanawha drainage, in Greenbrier River, not this species, but *C. decisum* is found.

C. rufum and *ponderosum* have no representatives on the Atlantic side, and clearly belong to the fauna of the upper Ohio River, although they probably belong to different parts of it.

IV. DECAPOD CRUSTACEANS: THE CRAYFISHES OF THE GENUS CAMBARUS.

The conditions presented by the distribution of the crayfishes have been discussed by the writer with regard to the state of Pennsylvania (Ortmann, 1906). These studies have been continued toward the south, and most of the facts given here for Virginia and West Virginia are new and add considerably to our previous knowledge. Of course, a certain ecological group is to be disregarded here, the burrowing crayfishes, for they do not live in open water, rivers or creeks, and do not depend in their distribution on drainage systems (*Cambarus carolinus* Er., *C. monongalensis* Ortm., *C. diogenes* Gir.).

A. The following river and creek forms are found on the WESTERN SIDE of the mountains.

Cambarus obscurus Hag. This species belongs to the upper Ohio system, from Moundsville, W. Va., in the Ohio, and from Fishing and Fish Creek upward. But it should be noted that subsequent investigations have shown that it goes a little farther down in the Ohio proper, for it is in the river at St. Mary's, Pleasants Co., W. Va. In the Allegheny River this species goes up to the headwaters (Coudersport, Potter Co., Pa.), and also in the tributaries (Red Bank, Mahoning, Crooked), except in the Kiskiminetas-Conemaugh, where it goes only to the mouth of the canyon at Blairsville, while it goes up into the upper Loyalhanna in Westmoreland Co. Thus the Conemaugh resembles the conditions seen in the more southern mountain tributaries of the Monongahela. In the latter this species goes only to the lower end of the canyons, and is not found in the upper parts (Youghiogheny, Cheat, Tygart), while in the plateau stream, West Fork River, it is found nearly to the sources (Weston, Lewis Co., W. Va.).

Cambarus propinquus sanborni Fax. As has been shown in my previous paper, this species takes the place of *C. obscurus* as the river-species below the lower boundary of the range of the latter. In the Ohio proper, *C. propinquus sanborni* has been found at Parkersburg, Wood Co., and at Ravenswood, Jackson Co., W. Va. It is also present in the tributaries of the Ohio in this region. An additional locality in the drainage of Middle Island Creek is McKim Creek, Union Mills, Pleasants Co., W. Va. It is in the Little Kanawha drainage in North Fork Hughes River, Cornwallis, Ritchie Co., and in the Little Kanawha River, Burnsville, Braxton Co., W. Va.[8] From the Kanawha drainage I have it from Elk River, Clay, Clay Co., and I collected it also in Mud River, Milton, Cabell Co., which is in the Guyandot drainage. Although I did not get it in the Big Sandy, it is surely there, for its type locality (according to Faxon) is Smoky Creek, Carter Co., Ky. (I could not locate this creek, but a place called Smoky Valley is in western Carter Co., and is in the Tygart Creek drainage; Little Sandy and Tygart Creek fall into the Ohio below the mouth of the Big Sandy.) Beyond this, this species disappears, and its place is taken by the next, but I have ascertained this only in Rowan and Fleming Cos., Ky.

Cambarus rusticus Gir. This is the river-species of Licking River, which flows into the Ohio below Cincinnati. The old record for this species, Cincinnati, would thus be confirmed. I found this species in Licking River proper at Farmer, Rowan Co., and in the tributaries, Triplet Creek, Morehead, Rowan Co., and Fleming Creek, Pleasant Valley, Nicholas Co., Ky.

Cambarus spinosus Bund. This is the representative species of *C. rusticus* in the upper Tennessee drainage, and I found it in Clinch River at Richland and Raven, Tazewell Co., Va. From this center of distribution it has crossed over into the Gulf and Atlantic drainages in Georgia and South Carolina, but this does not concern us here.

In a general way, these river crayfishes show the same geographical features as the bulk of the Ohio River shell fauna. The species

[8] These two localities are interesting, for they approach closely localities in the West Fork River, at Lynch Mines, Harrison Co., and Weston, Lewis Co., where *C. obscurus* is found.

of the propinquus group (*obscurus* and *propinquus sanborni*) have the same peculiarity as the Najades, in going up, in the rivers, only to the falls line in the mountain streams of West Virginia and southern Pennsylvania, while in the upper Allegheny they go up nearly to the sources. The fact that in the Kiskiminetas-Conemaugh they do not follow the Najades into Somerset Co., and that thus this river resembles the southern ones; and that then again the upper Loyalhanna conforms with the northern streams, is not very astonishing, for the Kiskiminetas system, being geographically intermediate, should also be expected to form faunistically a transition.

These crayfishes, however, differ from the Najades, in presenting a uniformity of the upper Ohio fauna only in so far as they are systematically closely allied, belonging all into the same natural group. But specifically they are quite sharply distinct, and *thus indicate, in their distribution, three faunistically different sections:* the upper Ohio is characterized by *C. obscurus,* farther down *C. propinquus sanborni* takes its place, and finally, beginning with Licking River, *C. rusticus* turns up, and this species has a representative also in the upper Tennessee, *C. spinosus.*

These conditions are important for the history of the crayfish fauna of the Ohio basin, and suggest, as I believe, that the Najad and the crayfish population of this system was not entirely subject to the same laws.

Cambarus bartoni (Fabr.). This is not a river species, but a species of the small and smallest creeks, going up to the very springs. It is found everywhere on the western side of the mountains, for instance, Blackwater River and Shaver's Fork, small runs tributary to Buckhannon River, upper New River drainage (Reed Creek), and small runs tributary to Clinch River. It is also on the Atlantic side (see below).

Cambarus longulus Gir. Is found, on the western side, only in the upper Kanawha drainage, Greenbrier and New Rivers, and also in the upper Tennessee drainage, Holston and Clinch. It is also on the Atlantic side (see below).

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B. Crayfishes of the Atlantic Side.

Cambarus blandingi (Harl.). This species has not been treated in my report on the Pennsylvanian crayfishes, but I have discovered subsequently that it is present in great numbers in the ditches of the Delaware meadows at League Island, Philadelphia. Its distribution is from New Jersey to Georgia, and in a slightly different form (var. *acutus* Gir.) it extends westward over the Gulf plain to Texas, and northward into the interior basin. The existence of related species chiefly upon the Gulf plain (Ortmann, 1905, p. 105) indicates that the *center of this species is in the southeastern United States,* and there is no question that it reached our section (from Virginia northward) by migration coming from the south. Thus it clearly belongs into the same group to which those Najades belong, for which we have located the center of dispersal in the southern parts of the Atlantic slope.

Cambarus limosus (Raf.) A species confined primarily to the lowlands and Piedmont region from New Jersey to Virginia, but which has gone up, in the Susquehanna and Potomac, into the mountains, possibly only secondarily. The facts of the distribution have been compiled in my former paper (1906, pp. 425 ff.), and the conclusion was reached (p. 432) that this is a form *belonging to the northern section of the Atlantic slope,* and that its connection with the western forms allied to it is around the northern end of the Appalachians. Thus it clearly falls into the same category with certain Najades mentioned above.

Cambarus obscurus Hag. This western species exists in the upper Potomac drainage. I have previously (1906) considered this as an accidental introduction, and more recently (1912*b*, pp. 51–54) I have parallelized this case with that of *Lampsilis ventricosa cohongoronta,* as due to artificial transplantation. Thus this is not an original feature of the Potomac drainage, and should be disregarded.

Cambarus acuminatus Fax. A species, known hitherto from the Atlantic drainage only in North and South Carolina, and also reported from French Broad River in North Carolina, tributary to the Tennessee. On the Atlantic side, however, this species extends farther north, and I have found it in Mason Creek, at Salem, and

in Tinker Creek, at Roanoke, Roanoke Co., Va. (Roanoke drainage), and in Mountain Run, Culpepper, Culpepper Co., Va. (Rappahannock drainage). Although differing from *C. blandingi* in not belonging to the coastal plain, but rather to the Piedmont plateau, or even the mountains, the direction of its distribution apparently was the same, from south to north, and thus it clearly *belongs to the southern element of the Atlantic fauna.* In the fact that the same species is also found in the Tennessee drainage, it resembles to a degree the case of *Eurynia constricta* and *vanuxemensis* among the Najades. But this may be disregarded for the present, for it does not concern the region under discussion.

Cambarus bartoni (Fabr.). All over the Atlantic side, also south of Pennsylvania, and I collected it myself, for instance, at Charlottesville, Albemarle Co., Va., and additional records are to be found in my former list of localities (1906, pp. 382–384). Here we have *a species of wide and general distribution both on the western and eastern side of the mountains,* going up into the very headwaters within the mountains. Thus it is clear that the divide has not acted as a barrier in this case, which I have explained by the exceptional means of dispersal possessed by this species in consequence of its ecological habits. This species is able to cross divides.

Cambarus longulus Gir. We have seen that this is in the upper Tennessee and the upper Kanawha, on the western side. On the eastern side it is a common form in the upper James drainage (Jackson and North Rivers). It also has been reported from the uppermost Shenandoah drainage, South River at Waynesboro, Augusta Co., Va.

This distribution clearly resembles that of *Symphynota tappaniana* among the Najades, and that of the genus *Anculosa* among the *Pleuroceridæ,* and there is no question that similar factors have contributed to bring this about, although in each of these cases certain peculiarities are observed. We shall devote more time to this farther below.

Chapter 4.

Summary of Distributional Facts which call for an Explation.

The above is the faunistic material which I have been able to collect. Comparing the facts observed in the different groups of freshwater animals discussed, several classes have been brought to our attention repeatedly, and they may be condensed under the following generalized heads.

I. Western Side.

1. *The Alleghenian divide actually forms a sharp faunistic boundary for a great number of freshwater creatures.* This is most evident for the forms of the interior basin, which go up to a greater or lesser distance in the upper Ohio drainage, but do not cross the divide. To these belongs the bulk of the *Najad*-fauna; the genus *Pleurocera* and the western species of *Goniobasis,* among the *Pleuroceridæ;* at least one species of *Campeloma* (*C. ponderosum*); and the group of *Cambarus rusticus* and *propinquus* of the crayfishes (which are closely allied).

In a general way *the interior basin fauna appears as a unit,* a number of species, chiefly *Najades,* being found uniformly in all parts of the Ohio drainage, from the upper Tennessee region to the upper Allegheny River.

2. Nevertheless there are indications of a *differentiation into several subdivisions,* which may be described as follows:

(*a*) The most sharply differentiated part is the *upper Tennessee region,* and to this belongs probably the whole Cumberland-Tennessee drainage. This is clearly seen in the *Najades,* in the *Pleuroceridæ,* and in the existence of a peculiar species of crayfish, *Cambarus spinosus,* belonging to the *rusticus* group.

(*b*) Another part comprises the *main fauna of the Ohio,* chiefly of the middle and upper parts, and its tributaries. This fauna shows preëminently the *uniformity* mentioned above, and goes from Licking and Big Sandy rivers in Kentucky to the upper Allegheny, including the Kanawha and Monongahela. In the Allegheny this fauna goes to the headwaters. But in the Kanawha and Monon-

gahela *it goes only up to a point at the lower end of the canyon* of the mountain tributaries. This latter feature is expressed in the *Najades,* and also in the genera *Pleurocera* and *Goniobasis* in the *Pleuroceridæ.* Also the crayfishes of the *propinquus*-group (*Cambarus propinquus sanborni* and *C. obscurus*) show it distinctly.

(*c*) A third part is the *region of the headwaters of the mountain streams,* tributary to Kanawha (New and Greenbrier) and Monongahela (Buckhannon, Tygart, Cheat, Youghiogheny). This fauna is chiefly characterized by *negative* features, by the absence of the typical forms of the upper Ohio (*2b*). But it also has some *positive* characters; for instance, the presence of *Symphynota tappaniana* in the upper Kanawha; of *Anculosa dilatata* in the upper Kanawha, Tygart, and Cheat; and of *Cambarus longulus* in the upper Kanawha. Of the various streams belonging to this region, each has some features of its own, and the elements have various relations to each other. It is very important to notice that most of the forms found in these streams are *represented, on the Atlantic side, by identical or very closely allied forms* (*Symphynota tappaniana, Strophitus edentulus, Anculosa dilatata, Cambarus longulus*). Other elements of this fauna belong to the general Ohio fauna (*Symphynota costata, Elliptio dilatatus, Alasmidonta marginata*), and just these have no closely allied forms on the Atlantic side (*Alasmidonta varicosa* is indeed allied to *A. marginata,* but as we shall see, it is not closely connected with the New River form).

It further should be noted that the New River shows relations to the upper Tennessee in *Cambarus longulus,* and possibly also in *Anculosa.* Further, the upper Kiskiminetas-Conemaugh drainage in Pennsylvania shows an intermediate condition between the more southern mountain streams and the more northern tributaries of the Allegheny; with regard to the *Najades* it conforms to the latter, with regard to the *crayfishes* to the former (excepting again the Loyalhanna).

II. Eastern Side.

1. The fauna of the Atlantic slope shows little evidence that it ever was an important, independent center of radiation. All forms belonging to it have more or less close relations to forms of the

interior basin (except *Margaritana*). A certain *uniformity* of this fauna is also expressed in two ways:

(*a*) By the *uniform and wide distribution of certain species,* indicating the possibility of intermigration between the various river systems;

(*b*) by the fact that the fauna of each river, disregarding a few lowland species, *goes up, in its bulk, into the mountains* and approaches closely the headwaters without appreciable depauperation.

2. There is a *differentiation of elements* within the Atlantic fauna, indicating different origin.

(*a*) A *southern element* pointing to a secondary center of radiation in the southern parts of the Atlantic slope is distinguishable. This center itself, however, lies chiefly outside of the region discussed here. Forms like *Lexingtonia,* like those of the *Elliptio complanatus* and *fisherianus*-group, *Alasmidonta collina, heterodon,* and *undulata, Eurynia constricta,* among the *Najades, Goniobasis virginica* and *symmetrica* among the *Pleuroceridæ, Cambarus blandingi* and *acuminatus,* among the crayfishes, belong here. These forms exhibit morphologically the greatest independence, and are possibly the oldest element in the Atlantic fauna. In some cases it is hard or impossible to connect them with types of the interior basin by more than general relationship.[9]

(*b*) In the *northern section of the Atlantic slope exists a group of forms,* which are more closely related to species of the interior basin and often must be regarded as their direct representatives. These are the *Najades* enumerated under group V. (p. 325), and the crayfish, *Cambarus limosus.* They all have their main range in the north, and toward the south they disappear sooner or later, and have no representatives in the south. Very often their southward range becomes restricted to the coastal plain.

(*c*) Further, there is a third group among the Atlantic forms. *These are either conspecific with western forms or extremely closely allied.* These are the *Najades* mentioned under VI. (p. 325), the

[9] It might be mentioned here, that these forms probably will be intimately connected with the Tennessee-Coosa problem, and their number will be greatly added to, when the fauna of the Carolinas and of Georgia is taken into consideration.

Sphæriidæ, the *Anculosa dilatata-carinata* group of the *Pleuroceridæ, Campeloma decisum,* and the crayfishes, *Cambarus bartoni* and *longulus* (I disregard, for the present, *C. spinosus* and *C. acuminatus,* as probably belonging to the Tennessee-Coosa problem, at any rate to a region lying to the south of the one which interests us here).

These forms generally go way up into the mountains, and practically meet there with the western range of the respective forms, so that the distribution seems almost continuous across the mountains, and suggests crossing of the divide.

There is great variety in the details of distribution of these forms, and two main groups may be distinguished: those with a more universal range on either side of the mountains, and those with a more restricted range on one or on both sides.

The above is a sketch of the chief distributional features, and we see that it is possible to group a number of cases under the same heads, which means to say that very likely similar causes have acted to bring about similar distribution. But before we begin the task to investigate the laws which governed these different types of distribution, it is necessary to recall to our mind certain fundamental facts with regard to the physiography of the Alleghenies.

Chapter 5.

Physiographical Facts. History of the Allegheny Mountain Region.

The origin and the development of the Appalachian or Alleghenian mountain system is rather well worked out (see McGee, 1888, Davis, 1889, Davis, 1891, Willis, 1896, Hayes, 1896, Davis, 1907), and we may assume that its general features are established. We do not need to go much into detail here, but certain phases in the mountain forming process should be brought out, which will be important for our present purpose.

A. Formation of Mountains by Upheaval and Erosion.

Lateral pression in a general direction from northwest to southeast, in Permian and Postpermian times, formed the ancient and original Alleghenian system, which consisted of a number of more or less parallel folds (anticlines and synclines) running in a northeast-southwest direction. These folds were pressed up against an old block of Archaic rocks lying to the east of them, the Old Appalachian belt of Davis (1907), now Piedmont plateau. They were piled up highest in the eastern part, close to the old Archaic rocks, but also in the southern parts the elevation was originally higher than in the northern, and in this section not only folds, but also faults, were formed.

As soon as this mountain system began to develop, erosion set in. The original drainage features conformed to the original structure; the highest elevation being well to the east, the divide was situated here, close to the old Archaic land, and the old rivers had to follow the structure of the mountains, running first between the parallel ridges in consequent, synclinal valleys, and finding their outlets at certain points in a westerly (northwesterly) direction, toward the interior basin. On the other side, toward the Atlantic Ocean, there were shorter streams, originating also on the highest elevation, running east and southeast, and reaching the sea after having traversed the belt of Archaic rocks.

The longitudinal streams on the western side of the divide began to carve out their valleys. But in addition, on top of the anticlines, anticlinal valleys began to develop, running parallel to the synclinal valleys, and very soon an important differentiation in the power of erosion of these streams became evident, which is due to the geological structure and succession of rocks of the mountains. The beds which compose them are all archaic and palaeozoic; but while the uppermost (Carboniferous) consist largely of hard sandstones, in the lower beds (Devonian and older) softer shales and limestones prevail. While the oldest rivers were running uniformly over sandstones, the anticlinal rivers, and chiefly those running on the highest elevations, had the best chance to cut first through the sandstones and reach the softer beds below. After this, these streams working

in a less resistant material, had the advantage, and thus the anticlinal valleys were more deeply excavated than the synclinal valleys. This process advanced farthest in the eastern section of the mountains, so that what was once the highest elevation became finally a deeply excavated valley.

This general process was repeatedly interrupted by the fact that the whole region was reduced to base level. One of these periods of base level conditions is most important to us, that of Cretaceous times, when most of the mountain region was a peneplain, little elevated above the sea, but with certain hills (monadnocks) standing above this level. In Postcretaceous times a reëlevation took place, and the rivers began their work again, according to the same laws, but with complications due to the base-level period. During the latter, they had acquired courses across the strike of the mountains, and these were inherited by the later rivers, and often they were compelled to cut across hard rocks, thus forming so-called water gaps, which have no apparent connection with the original geological structure.

The difference in the erosion has produced a physiographical differentiation within the whole system. In the western parts, where the Pre-Carboniferous soft rocks have not been reached, either synclinal valleys are present, or the drainage system is independent on the structure, irregular or dendritic. This section has been base-leveled rather completely in the past, and thus it is of the character of a plateau, and has been called the *Alleghenian Plateau.* The eastern parts, which were originally much higher, have been much cut into by the anticlinal streams, which have carved out broad limestone valleys, with high ridges of harder rock between them, so that this region has a more mountainous character, and is known as the *Allegheny Mountains* proper. Within these mountains, farthest to to the east, where there was once the highest elevation, an exceptionally broad valley has been excavated, called the *Great Allegheny Valley.*

Thus we have, going from west to east across the mountains (see Plate XII.): (1) *The Allegheny Plateau;* (2) *the Allegheny Mountains,* with numerous ridges and valleys, the most eastern valley being

the *Great Allegheny Valley,* then follows, east of the mountains, a much older section of the country; (3) *the Piedmont Plateau,* a peneplain, the remnant of the Old Appalachian land; and finally toward the ocean comes an additional physiographic division, (4) the *Coastal Plain,* lying between the Piedmont Plateau and the sea, of various width, which consists of marine deposits of much younger geological age (Cretaceous and Tertiary) (see McGee, 1888, Powell, 1896, Davis, 1907).

In the southern Appalachians this division is somewhat modified. The boundary between 2 and 3 is more developed (Blue Ridge) and is called the *Appalachian Mountains,* while no. 2 has more of a valley character and is called *Appalachian Valley.* No. 1 is called *Cumberland Plateau* (see Hayes, 1899, Pl. 1).

The boundary between the *Coastal Plain* and the *Piedmont Plateau* is well marked by an escarpment forming a falls line for the streams traversing the Piedmont Plateau. The *Allegheny Mountains,* and chiefly the *Allegheny Valley,* are marked off from the *Piedmont Plateau* by the flank of an anticline, consisting largely of archaic rocks, known in Virginia as *Blue Ridge,* and continued into Pennsylvania as *South Mountain.* But farther north this ridge becomes obscure, and Piedmont Plateau and Allegheny Valley are more or less indistinct. In southern Virginia the Blue Ridge widens out and becomes a more important member of the system, finally reaching in North Carolina the highest elevation (see above). The *Great Allegheny Valley* is very distinct northwards, in Pennsylvania, Maryland and northern Virginia, forming a broad and flat limestone valley, and is sharply differentiated from the more western mountains and valleys. Farther south it merges more or less with the mountain region, which consists of several broad and flat limestone valleys, separated by longitudinal ridges formed by monoclinal harder rocks.

The boundary between the *Allegheny Mountains* and the *Allegheny Plateau* is well marked in Pennsylvania and Maryland by the western flank of an anticline, known as *Allegheny Front.* Farther south this may be traced to a certain distance,[10] but then, in West

[10] Willis, 1896, p. 186 (also Abbe, 1899, p. 70), use the name Allegheny Front much farther South, for the escarpment west of Bluestone River: this

Virginia, the mountain-type of erosion encroaches upon the plateau, and, for instance, the valley of the upper Tygart and Greenbrier valley are largely anticlinal valleys of the mountain-type (see Fontaine, 1876, p. 9), so that the eastern edge of the Allegheny Plateau is pushed back westward. In the region between James and New River and beyond (toward the southwest), conditions become more complex by the development of faults, and here the eastern edge of the plateau (Cumberland Plateau) is formed by a tremendous fault, which brings the Carboniferous down to about the same level with the Cambrian. (See maps and profiles in Rogers, 1884; also geological map by Willis, 1912; as to the faulting, see Lesley, 1865; Stevenson, 1887; Powell, 1896, p. 79.)

B. Stream Capture.

There is yet another factor which contributed to make the structure of the Alleghenies more complex. We have seen that the original divide of the waters probably was well to the east, not far from the old Piedmont land. It is clear that from this divide the way to sea-level (the Atlantic Ocean) was short and direct, while westward it was long and devious. This produced a much steeper grade of the eastern streams, and consequently the eroding power of the latter must have been much greater than that of the western streams. The eastern rivers had thus the first chance to saw through the divides westward. This resulted in the general law that the Atlantic streams have the tendency to cut into and to encroach upon the region which originally drained westward. This general law is not without exceptions, but such are rare.

Also the Atlantic streams have been subject to stream capture between themselves; Campbell (1896, p. 675) points out the unsymmetrical development of their basins, with the divides shifting toward the southwest; the Susquehanna developed at the expense of the Potomac, the Potomac at the expense of the James, the James at that of the Roanoke. Similar conditions probably existed on the western side.

is correct only in so far as this escarpment represents the eastern boundary of the Allegheny Plateau, but it does not correspond to the same structural line as the Allegheny Front in Pennsylvania.

This stream piracy or capture must have gone on all through the history of the mountains; but the evidence for the older cases is largely lost on account of the base level conditions prevailing at various times. Only more recent (Postcretaceous) cases are more or less clear. But in a general way the present rivers indicate that stream capture has been most effective in the northern parts of the Alleghenies, and, toward the south, the various rivers show this phenomenon in a lesser degree. (Davis, 1889; Hayes and Campbell, 1894, p. 102; also Campbell, 1896.) In addition, these processes were modified by a tilting of the reëlevated peneplain in opposite directions in the north and south (Powell, 1896, p. 79).

C. Present Condition of Drainage. (See Plate XII.)

At the present time we have only in the southern Appalachians the remnants of the primitive condition of the drainage, streams running toward the west, with their sources near or in the Blue Ridge, well to the east. This is the case in the Tennessee and New River region. New River is a good example of this, and we may safely regard this river as representing most nearly the original drainage features (Davis, 1907, p. 732: "There is not another river in the whole Appalachian region that so well preserves its ancient course.")[11]

Following the Allegheny Mountains and the Allegheny Valley northward, we meet streams draining more and more in an easterly direction, first the Roanoke, then, in succession, the James, Potomac and Susquehanna, and it is interesting to notice that the first one

[11] Davis means here by "ancient" preëminently the Pretertiary time. But probably the present New River is not the oldest line of discharge out of this region. Using the same methods as used by Davis (1889) for the construction of the old Anthracite River in Pennsylvania, we would obtain an old river running West in the depression between two elevations (monadnocks), along which now runs the Chesapeake and Ohio Railroad (between Covington and Hinton, see Pl. XII. and profile, Pl. XIV., fig. 2). Probably the fault on the western side of Peters Mountain also played a part in defining this oldest line of discharge. The present New River would then be a later (but probably also Pretertiary) feature, and would have about the same relation to the old river, as the present Susquehanna has to the old Anthracite River, after its reversion.

occupies only the valley, and very little of the mountains, while every succeeding one cuts farther back into the mountains (Campbell, 1896, p. 675).

In the region of the uppermost Roanoke there is a good instance of more recent stream piracy. The headwaters of the North Fork are running first in a southwesterly direction in a valley, which is clearly continued toward New River; but just north of Christiansburg this fork makes a sharp bend, cuts through Paris Mountain, and flows then eastward and northeastward. It is clear that the Roanoke has captured here a former tributary of New River (see Campbell, 1896, p. 674, and our map, Pl. XII., and profile pl. XIV, fig. 1).

James River has cut much farther into the Allegheny Mountains. It is doubtful whether the original streams in this region belonged to New River. According to Hayes and Campbell (1894, p. 110) no important shifting of divides has taken place in this region during the Tertiary cycle, although, as we have seen, Campbell (1896) assumes stream piracy between James and Roanoke. This region is extremely complex in structure and has little been investigated.

Coming to the Potomac drainage, we observe that this river has cut clear across the mountains, and has reached, in northeastern West Virginia and in western Maryland, the western boundary of the Allegheny Plateau, Allegheny Front, and at one point has even cut through this and encroached upon the Allegheny Plateau, draining now a longitudinal synclinal valley. (See our map, Pl. XII., and profile pl. XIV, fig. 2.) As to the former drainage in this region very little is known. But according to Campbell (see above) the Potomac has robbed, in the region of the mountains, James River, and in one case, in the Shenandoah Valley, we have instances of more recent stream piracy during the Tertiary cycle. The Shenandoah is a rather recent stream, which has captured in succession several older streams, running originally independently through Blue Ridge eastward (see Davis, 1891, p. 576, and Abbe, 1889, p. 68).

The Susquehanna in Pennsylvania has progressed farthest in the capture of western streams. It has not only cut clear across the mountains, but also has invaded a large section of the plateau, which

originally drained to the westward (see Plate XII.) The primitive drainage features of this region have been worked out by Davis (1889), and according to him this whole region was once drained by the ancient Anthracite River, running in a northwesterly direction through what is now the anthracite basin, its sources being situated well to the east, in the Kittatinny highland. The upper part of this river was first reversed, so that it discharged southeastward (direction of present Schuylkill), and then the Susquehanna encroached upon this system, becoming finally the master stream in Central Pennsylvania during Jura-Cretaceous times. The final step in the development of this drainage was the capturing of the plateau drainage, but also this falls largely into Pretertiary times. That the Susquehanna encroached also southwestward upon the drainage of the Potomac has been mentioned above, and this probably is the chief change of this system which belongs to the Tertiary time.

D. History of the Western Drainage.

At the present time all western streams are finally united into one great system, that of the Ohio, which finally runs into the Mississippi and the Gulf of Mexico. In the past this was different, and we know now that the present system is of comparatively young age, that the Ohio is a recent stream, and that the former drainage features of this region were entirely different. According to the investigations of a number of writers (for instance, Foshay, 1890; White, 1896; Leverett, 1902; Tight, 1903), there was no Preglacial Ohio River, but in its place there was a system of northward flowing streams. In the region under consideration two of them are well established: the *Old Monongahela* in western Pennsylvania and northern West Virgina, and the *Old Kanawha* in West Virginia (the Big Sandy belonging to the latter). How the conditions were farther down is somewhat doubtful, but there might have been a third river of the same general character (Licking-Miami, or *Cincinnati River,* see below).

The advancing ice of the Glacial period shut off the outlet of these rivers, dammed them up, converted them into lakes, and finally the waters were forced to seek another outlet, and the general slope

of the country and the direction of the edge of the ice made them find this outlet in a southwesterly direction, thus connecting the old Preglacial systems by a new river, which was the beginning of the present Ohio. *The Ohio thus was formed during Glacial times.*

The northward flowing Preglacial rivers were connected by a master stream called *Erigan River,* running in a direction about parallel with the direction of the present St. Lawrence. There is some dispute as to the direction of this old river (northeast or southwest), but the evidence preponderates which assigns to it a northeasterly flow. The present writer has shown also (1906, p. 429) that certain facts in the distribution of crayfishes point to this conclusion, that is to say, that this drainage finally was eastward into the Atlantic Ocean. This question will be discussed farther below.

E. Mutual Connection of the Atlantic Streams.

The present Atlantic streams, Delaware, Susquehanna, Potomac, James, Roanoke, are quite independent from each other, and discharge separately into the sea, so that no direct intercommunication of their waters seems possible. However, we have seen that their headwaters interlock closely, and that it is probable that in the past stream capture has taken place between them in the region of the Allegheny Mountains (see above the quotation from Campbell, 1896, p. 675). In their course across the Piedmont Plateau these streams are at present generally well separated, but farther to the east, where they enter the region of the Coastal Plain, they reach a physiographical section of a character which permits frequent interchange of the waters. In addition, we know that the Coastal Plain extended, at certain times, farther seaward, and that the present Delaware and Chesapeake Bays and also the estuaries of the other Atlantic streams represent drowned river valleys, so that probably in the past this interchange of the waters took place on a larger scale (see LeConte, 1891; Powell, 1896, p. 73; Spencer, 1903; Davis, 1907, p. 717).

Thus the Atlantic streams were not always isolated from each other, and in the past, as well as in the present, an intercommunication of their waters was possible, chiefly on the Coastal Plain, which, of course, also must have permitted an exchange of the faunas. The importance of this will be understood below.

Chapter 6.

Explanation of Distributional Facts.

We are now ready to study the faunistic facts with regard to their genesis, and shall take them up according to the classification given above (Chapter 4, pp. 338–341).

Fact I., 1.

The fact that the eastern and western faunas are sharply distinct, and that the Allegheny system actually forms a sharp faunistic barrier of the freshwater faunas, does not need any comment, for mountain ranges generally are most apt to act as divides between rivers and their faunas unless the elements of these faunas have exceptional means of dispersal (by transport). The very fact that the western forms generally have not crossed the divide, nor have the eastern forms, indicates that among three of the groups discussed here (Najades, Pleuroceridæ, Crayfishes) no such exceptional means of dispersal have acted to any considerable degree. However, as we shall see farther on, there are some exceptions.

One point, however, deserves special mention. There have been periods of general base-leveling, the last important one belonging to the Cretaceous time. It is very likely that at this time the barrier was not so well marked, and that a more general interchange of the faunas was possible. If any cases in the present distribution are to be traced back to this time, there are very few of them, and the majority of the cases, chiefly of the *Najades,* does not show any evidence of this. This means to say that probably the bulk of the *Najad*-fauna of the Appalachian River systems *is not older than the Cretaceous time, probably largely Postcretaceous.*

This is an important conclusion in view of the fact that we know from fossil remains that *Najades* existed in North America in Jurassic time and possibly even earlier. But it should be noted that these fossils are known practically exclusively from the western parts of the continent. This, however, cannot be followed up any farther, since it would lead us too far away from our present purpose.

While thus the western fauna could not cross the Alleghenian

barrier, we further have noticed the fact that it forms distinctly a unit from the upper Allegheny River at least to Licking River in Kentucky. It is hardly necessary to discuss this, since the present conditions sufficiently explain this uniformity; all these rivers, running westward, are united into one master stream, the Ohio. Also the system of the Tennessee, which has much in common with the Ohio, finally unites with this river.

However, when we come to study the origin of this fauna and to consider the fact that the Ohio drainage in its present form is a modern feature of our hydrography, we have to ask the question, what the old conditions were?

There is hardly any doubt that the uniform *Najad*-fauna of the upper Ohio basin is, in its origin, connected with the origin of the Ohio River, that is to say, that it is not older than the Glacial time, probably largely Postglacial. The fact brought out above, that from the upper Allegheny downstream this fauna becomes richer, and that the number of species increases steadily farther down (from 47 in Pennsylvania to about 60 or more in the vicinity of Cincinnati), makes it certain that the center of dispersal of this fauna was in the region of the lower Ohio, probably also including the Tennessee system, and that *this fauna migrated upstream in Glacial and Postglacial times* as soon as the present Ohio was formed, depauperating gradually in the direction toward the headwaters.

Fact I., 2, (a).

The fauna of the upper Tennessee is very strongly marked. Nevertheless it shows distinct affinities to the Ohio fauna. We have studied only a very small part of it, and it is well known that farther down in the Tennessee and also in the Cumberland River drainage, this fauna becomes still richer.

Without a closer and more exhausting study of this fauna it is impossible to express any definite ideas as to the origin of it. Thus we have to dismiss this topic here and it is sufficient to say that probably this fauna represents the common ancient stock, and the great center of radiation, not only of the interior basin fauna, but also of that of the Atlantic slope and the Gulf region. That the Ohio

River fauna probably is a branch of this fauna has been indicated, and the migration was in this case from the lower Ohio upstream. The question remains whether the upper Ohio received also elements from the upper Tennessee by another route, and this question is suggested by the fact that the headwaters of Clinch and Holston rivers on the one side and those of Big Sandy and New River approach each other very closely and frequently interlock in the mountains.

It is known (see Campbell, 1896, p. 670) that the headwaters of the Big Sandy are preparing to capture the headwaters of Clinch River in Tazewell Co., Va., in a region where the latter river has a rich and characteristic fauna. The Big Sandy tributaries have already reached the valley limestone and may have already deflected some of the smaller tributaries of the Clinch. In the *Najad*-fauna of the Big Sandy (see p. 309) there is no evidence for this. But the fact that a species of *Pleurocera, Pl. unciale,* is common to the Clinch and the Big Sandy, possibly supports this assumption.

There is also little evidence for a communication between the upper Tennessee and New River except the existence of the *Pleurocerid*-genus *Anculosa* in both systems and the presence of an identical species of crayfish, *Cambarus longulus.* The two species of *Najades,* which are common to both systems, *Elliptio dilatatus* and *Alasmidonta marginata,* are without convincing value, since they are found all over the interior basin, and of *Elliptio dilatatus* there is surely quite a different, dwarfed race in the New River, while the Clinch contains the normal form. In view of the tremendous contrast between the upper Tennessee and the New River faunas, it is not very likely that there was any extended migration at any time across this divide, or that there was any important shifting of this divide. This is in accord with the general history of these streams. According to Campbell (1894, p. 110), the divide between New and Holston rivers is a narrow col characteristic for a long-maintained divide, and Hayes (1896, p. 330) says that the headwaters of the Tennessee, running generally over softer rocks, had a tendency to encroach northeastward upon the upper Kanawha system, but that this tendency was counterbalanced by the fact that New River also cut its own channel deeply into the (harder) rocks of its own trans-

verse valley. If there was any stream piracy in the past it would have been the Tennessee, which had the advantage over the New River, so that the latter could not receive anything from the former.

This seems to be supported by the general character of the fauna. The two cases mentioned above (*Anculosa* and *Cambarus longulus*) will be taken up again further below.

Fact I., 2, (b).

The main fauna of the Ohio reaches, as we have seen, in the Kanawha and the mountain tributaries of the Monongahela only up to the lower end of the falls-line, marked by a canyon. It is clear that here the upward migration of the Ohio fauna is checked by the physiographical character of these streams. The upper Allegheny and its tributaries are Plateau streams, originating upon the Allegheny Plateau at elevations of about 2,000 feet (see pl. XIII, fig. 1), and the West Fork River of the Monongahela falls into the same class (see pl. XIII, fig. 2), and in these streams the fauna goes way up. But in the case of the tributaries of the Monongahela, Youghiogheny, Cheat, Tygart, and also in New River (including Greenbrier) of the Kanawha system, the sources are in mountains of 3,000 to over 4,000 feet elevation. These rivers have a very steep grade, and in a certain region they all run through a more or less well developed canyon. The lower end of this canyon forms the upper boundary of the Ohio River fauna in the Youghiogheny at Connelsville, Pa., in the Cheat at Mont Chateau, W. Va., in the Tygart at Grafton, W. Va., in the New River at Kanawha Falls, W. Va.[12] (Compare our profiles, Pl. XIII., fig. 2, and Pl. XIV., fig. 1.)

We have to regard it as an ecological fact among the *Najades* (and some other freshwater Mollusks, for instance, the genus *Pleurocera*), as well as in the river-crayfishes (Ortmann, 1906, p. 412), that they do not like rough water and unstable, shifting bottom. The canyons of the falls-line of these rivers are, next to their upper-

[12] Of course, exceptional cases, where single species have found a way up and through the canyon, may be disregarded. Such are the cases of *Quadrula tuberculata* and *Rotundaria tuberculata* in the New River at Hinton, and probably also of *Symphynota costata* in the Tygart at Elkins.

most headwaters, the roughest parts of them, characterized by firm bedrock bottom covered with loose stones and boulders, often shifting, chiefly during flood stages. Such conditions are entirely unfavorable to crayfishes and *Najades* (the latter generally demanding sand and gravel, which is *firmly packed*), and thus we have here an *ecological barrier to the upstream migration of the Ohio fauna,* which is absent, for instance, in the upper Allegheny.

The fact that this fauna is here checked by a *modern* physiographical feature confirms the assumption that the upstream migration of it falls in a rather recent (Glacial and Postglacial) time.

Excepting these mountain streams just discussed, the uniform Postglacial upper Ohio fauna comprises all the headwaters of the Ohio (Allegheny and Monongahela), and further all the tributaries in West Virginia; also the fauna of the Big Sandy belongs undoubtedly here, and we know that this river once was closely connected with the Old Kanawha River (Tight, 1903), and that its history was similar to that of the other rivers, which are ancestral to the upper Ohio system. This is somewhat different in the case of Licking River in Kentucky. Leverett (1902, p. 109) unites this river with the Preglacial lower Ohio (and with the Kentucky, Cumberland and Tennessee rivers). If this is correct, we should expect in this river the Tennessee-Cumberland fauna; but there is no trace of it here,[13] and the Licking fauna is entirely of the same character as that of the rest of the upper Ohio, as far as it concerns the *Najades.* Of *Pleuroceridæ* a new species turns up here, but this material is too unsatisfactory. But on the other hand a peculiar crayfish is found in the Licking, *Cambarus rusticus,* which distinctly points to the west. But since also Monongahela and Kanawha are characterized by different (although closely allied) species of crayfishes, Licking River also in this particular falls in line with these other streams.

The physiographical evidence with regard to the history of Lick-

[13] See p. 309. The fauna is not completely known, but according to my collections, only one species turns up, which is absent in other parts of the upper Ohio drainage discussed here: *Anodontoides ferussacianus.* All the rest is typically upper Ohioan. It also should be noted, that one species, *Lampsilis luteola,* is present here, which is absent in the Cumberland-Tennessee fauna.

ing River is yet obscure. As we have seen, Leverett unites it with the Preglacial lower Ohio. But the fauna of the river, especially of the *Najades,* strongly points to the fact that Licking River has a similar history to that of the Kanawha and Monongahela, that is to say, *that it was in Preglacial times a northward flowing stream, which might have belonged to the old Erigan River* (see above, p. 349), and that it had no connection with the lower Ohio and Tennessee-Cumberland. And indeed this is the assumption made by Tight (1903, see map, pl. 1), who gives to the Licking and Kentucky rivers (under the name of *Cincinnati River*) a northward flow in Preglacial times.

Thus, in this case, zoögeographical evidence is in favor of Tight's assumption, and this is an interesting instance, where zoögeography contributes to the solution of a physiographical question.[14]

We have repeatedly emphasized, that the upper Ohio fauna is a unit, and rather uniform all over the terrritory it occupies, with the only qualification, that it slowly depauperates in an upstream direction. This is true, in the first line, of the *Najades,* but it may be correct also for certain *Pleuroceridæ,* at least such forms which follow mainly the large rivers (certain species of *Pleurocera,* as for instance, *Pl. canaliculatum*). But in other groups, some minor differences within the upper Ohio fauna are noticed. Some evidence of this is seen in the *Pleuroceridae* of the smaller rivers, the Allegheny, Monongahela, Kanawha, Big Sandy and Licking, each of which has different species of *Pleurocera* and *Goniobasis* (provided such are present at all). But these conditions require further study, chiefly with regard to the affinities of these forms. But it is interesting to note, that it seems that the conditions known to exist among the crayfishes are duplicated here.

In the case of the crayfishes, I have pointed out (1906), that there are two different species in the upper Ohio drainage, and that

[14] This should be studied farther, chiefly with regard to the additional question regarding Kentucky River: If Tight's and our view is correct, Kentucky River should conform in its fauna to that of Licking River and the upper Ohio in general; if it belongs, however, to the lower Ohio, it should contain elements of the Cumberlandian fauna. Unfortunately the Kentucky fauna is practically unknown.

their distribution undoubtedly is *correlated with the old Preglacial drainage systems. Cambarus obscurus* belongs to the old Monongahela River, while *C. propinquus sanborni* indicates, in its present distribution, the old Kanawha River. This theory has been fully confirmed by my subsequent investigations, which have shown that *C. obscurus* actually is the river-species of the Monongahela in West Virginia, up to the headwaters of the Plateau stream West Fork River, while to the south of this, in the little Kanawha, Big Kanawha, Guyandot, and in the corresponding part of the Ohio proper, *C. propinquus sanborni* is found. This latter form probably is also in the Big Sandy, and a few smaller streams to the west of this in Kentucky, all belonging to the Old Kanawha of Preglacial times.

The additional information was obtained that in Licking River another species is found, *C. rusticus.* This means, that this river had a more isolated position from the others in Preglacial times, although belonging probably also to the old Erigan drainage.

While thus the *Najad fauna* of the upper Ohio follows in its distribution the modern features of this river, and while we are to conclude, for this reason, that it is largely *Postglacial,* the *crayfish fauna* indicates *Preglacial* conditions. And further, it seems that, among the *Pleuroceridæ,* we have both elements represented, but, unfortunately, the natural affinities of this group are yet too obscure to permit any final conclusions.

Fact I., 2, (c).

In the headwaters region of the mountain streams tributary to the Monongahela and Kanawha, above the canyon, there is generally a section, where these rivers are less rough, and run more quietly in elevated, often broad valleys (compare profiles, Pl. XIII., fig. 2, pl. XIV., fig. 1). As has been said, the fauna of these parts is chiefly characterized by the *absence* of the common upper Ohio types. Nevertheless we have a small number of forms here, which are more or less characteristic.

These forms are not uniformly present in all these rivers, and their distribution may be tabulated as follows:

1. Monongahela drainage—

a. Youghiogheny: *Strophitus edentulus.*

b. Cheat: *Anculosa dilatata.*

c. Tygart: *Symphynota costata, Strophitus edentulus, Anculosa dilatata.*

2. Kanawha drainage—

a. Greenbrier: *Elliptio dilatatus, Symphynota tappaniana, Alasmidonta marginata, Anculosa dilatata, Cambarus longulus.*

b. New River: The same as in Greenbrier, and in addition (at Hinton only): *Quadrula tuberculata* and *Rotundaria tuberculata.*

Two classes may be distinguished among these: those which have no relations on the eastern side, and those which are represented there by identical or very closely related forms. The former are: *Symphynota costata* of the Tygart, and *Quadrula tuberculata, Rotundaria tuberculata, Elliptio dilatatus,* and *Alasmidonta marginata* of the upper Kanawha. These are species rather generally distributed in the upper Ohio region, and they probably belong to this fauna, representing forms, which for certain special reasons, possibly by mere chance, were able to ascend somewhat higher in the mountain streams than the bulk of the Ohio fauna.

The other forms, *Symphynota tappaniana, Strophitus edentulus,* and the crayfish *Cambarus longulus,* are represented on either side of the divide by the identical species, while in the case of *Anculosa* two extremely closely allied species, *A. dilatata* and *carinata,* are found west and east of the divide.

These latter facts are very interesting, and touch upon the question, whether and how it was possible that certain forms of freshwater life were able to cross the divide. For the present, we shall only indicate this problem, but we shall take it up again, when we come to speak of the Atlantic forms, which are more or less nearly related to western ones (see below, under fact II., 2, *c*).

It also should be pointed out, that an additional interesting question is involved here. We have seen, that the general Najad-fauna of the Ohio, which goes up to the lower end of the canyons, is of Postglacial age. This fact suggests, that also the falls line of the canyons is comparatively recent, and that it marks a last rejuvena-

tion of these streams in consequence of a reëlevation of the country. According to Foshay (1890, p. 400) and others, this rejuvenation is of Postglacial age. *Thus we might expect to find in these upper parts of the mountain streams, the remnants of the fauna which existed in these rivers in Preglacial (Tertiary) times.* I have no doubt, that at least some of these are Tertiary elements, and possibly just those which are found on either side of the mountains might belong to them. However, this fauna is too fragmentary, to be sure about this, and it is quite evident, that also in Tertiary times not the whole of the fauna of these rivers went up to near the headwaters. Thus we have to wait till additional evidence with regard to the Tertiary fauna of the headwaters of the Erigan system is forthcoming.[15]

FACT II., 1, (a).

It has been seen, that there is a certain amount of uniformity in the Atlantic fauna, in spite of the fact that the Atlantic river systems are quite isolated from each other. In fact, most of the Atlantic species are not restricted to a single drainage, but are found in several, often practically in all of them. This means, that there is or there was the possibility of an intercommunication of the faunas of these rivers, and the question arises, how this was brought about.

All these rivers, after having traversed the Piedmont Plateau, run for a greater or lesser distance through the Coastal Plain. This plain is little elevated above sea-level, and consequently the rivers are sluggish here; there is considerable deposition of material in this region, and a great tendency toward a change in the river channels: the rivers are practically at base-level. It is a general rule, that in a country approaching base-level, the intercommunication of neighboring rivers is greatly facilitated (see Adams, 1901, p. 842), and that consequently a wide distribution of the fauna is favored.

[15] The best evidence would be fossil forms from the high river terraces. Such do exist, but the remnants are too poorly preserved, to be of any value. It should also be noticed, that there is a number of species in the upper Ohio drainage, which distinctly avoid the larger rivers: also these might be elements of the old Tertiary fauna. It is interesting, that several species of the present fauna of the mountain streams fall into this class, namely: *Symphynota costata, Alasmidonta marginata, Strophitus edentulus.*

There is no question that this is one of the factors, which has largely brought about the more or less universal distribution of the species of the Atlantic slope, and has permitted their spreading from one river system into others, notwithstanding the contrary opinion of Johnson (1905), who does not believe that "river captures" are to be assumed in this region, but that passive transportation accounts for the universal distribution of certain Najades over the Atlantic slope. Indeed, it is not river capture in the strict sense, which caused the present conditions, but what Adams (*l. c.*) calls "removal of barriers" in a country approaching base-level. This is also practically the opinion of Simpson (1893, p. 354, footnote 2), when he says, that shells may migrate from river to river "across overflowed regions near the sea, in times of floods." (We always must bear in mind that the migration was by the help of fish, which carried the larvæ.)

This lowland zone reaches all the way up the coast to New York state. But we know, that at certain times it extended even farther north, when the continent stood at a higher elevation, and when the coastal plain was wider than at present. We must also consider, that at other times the coast was more submerged than now, and that then also the Piedmont Plateau was more or less at base-level, offering the same conditions favorable to a migration of the fauna.

Moreover, we have seen, that there was stream-capture in the region of the mountains, and that the northern rivers had a tendency to encroach upon the southern. This should have caused a migration of southern forms northward in the mountain region, but not of northern forms southward. There is indeed evidence of it in the fact, that forms with a northern center of dispersal (those falling under II., 2, *b*) availed themselves, in their southern dispersal, of the coastal route, for instance, *Lampsilis radiata, cariosa, ochracea* and *Cambarus limosus,* for they become more and more restricted to the lowlands in the southern parts of their range. On the other hand, those forms, which have a more general distribution, also in the mountain region, are chiefly southern in their origin, as for instance: *Elliptio complanatus, Alasmidonta undulata, Goniobasis virginica,* and these may have availed themselves, in their

northward dispersal, also of stream piracy in the mountains. In a few cases, the latter probably was the prime factor in the dispersal, chiefly in the case of *Anculosa carinata.*

Thus there is no difficulty in admitting the possibility of the dispersal of the Atlantic fauna over more or less of the whole region. The facts in the distribution of the *Najades,* as well as in the *Pleuroceridæ,* and in the *crayfishes* support this assumption. But the other fact, that certain forms of the Atlantic slope did not reach a universal distribution, and were apparently obstructed in their dispersal at certain points, needs further discussion. This is a more difficult problem, but, as far as possible, it will be taken up below.

Fact II., 1, (b).

Aside from certain species (Najades: *Elliptio fisherianus, Anodonta cataracta* and *implicata, Eurynia nasuta, Lampsilis radiata, cariosa, ochracea,* and the crayfish *Cambarus blandingi*), which are more or less typically species of the lowlands or the great rivers, the fauna of the Atlantic streams is rather uniform, in each system, from the Piedmont Plateau upward into the mountains, to near the sources. (See list no. 23 of Najades, and also *Goniobasis virginica, Anculosa carinata, Cambarus limosus.*) That is to say, the fauna does not deteriorate, or very little so, in an upstream direction. This differs strikingly from the conditions on the western side, where a gradual decrease of the number of species toward the sources is the rule, or where we even observe a sudden disappearance of species at certain points in the mountain streams.

The explanation of this fact is found, as I believe, in a general physiographical character of the Atlantic streams, which is best expressed by their profile (see our profiles on Pl. XIII., and Pl. XIV., fig. 1). We see that the profiles of the Atlantic streams are more nearly normal (Abbe, 1899, p. 61, fig 3; of course we must disregard the falls line at the eastern edge of the Piedmont Plateau). This profile indicates comparative stability, with the slope steepest at the headwaters, decreasing rapidly just below headwaters, and then gently farther down. These streams are more mature than those of the western side. On the eastern side, new cycles of ero-

sion, of rejuvenation, indicated by falls or rapids beginning somewhere in the lower parts, have had time to work back to the headwaters (the cycle being completed), while on the western side these cycles, at least some of them, are not quite finished, and are indicated by falls and rapids lying at various distances below the headwaters (see profiles, Pl. XIII., fig. 2, Pl. XIV., fig. 1).

It does not require any further discussion to see that this difference of the eastern and western streams is finally to be referred to the different general slope of the rivers, the former being short and more direct in their course to the sea, and thus working faster.

The consequence is, that the aquatic life of the lower sections of the Atlantic streams finds congenial conditions up to near the headwaters, since the conditions are more nearly uniform all along the stream. Only close to the headwaters, there is a rather sudden change, and here the fauna deteriorates also quite suddenly.

Fact II., 2, (a).

We have seen that a *differentiation of elements* within the Atlantic fauna is indicated, and that first of all, a *southern element* is clearly distinguishable. A number of *Najades* belong here, the snail *Goniobasis virginica,* and two crayfishes, *Cambarus blandingi* and *acuminatus* (see p. 340).

In all these forms it is evident that they have their center of radiation somewhere in the southern section of the Atlantic slope (Carolinas, Georgia), whence they migrated northward (see Simpson, 1896*b,* p. 337). But we notice that the different forms have advanced northward to different points. Some of them spread all over the Atlantic slope, northward even beyond the section discussed here; so, for instance, *Elliptio complanatus, Alasmidonta undulata* (possibly also *Alasmidonta heterodon*), which go to New England; *Goniobasis virginica* has reached the state of New York, and *Cambarus blandingi* (restricted to the lowlands) has reached middle New Jersey.

Others do not go so far. *Elliptio fisherianus,* a lowland form, goes northward to the lower Delaware; *Elliptio productus* to the Potomac; *Elliptio lanceolatus* and *Cambarus acuminatus* to the

Rappahannock; *Lexingtonia subplana, Alasmidonta collina, Eurynia constricta* to the James; and *Goniobasis symmetrica* to the Roanoke.

This peculiar fact, that the southern elements in the Atlantic fauna have advanced to different distances northward, is hard to explain. The general tendency to migrate northward is understood by what has been said under II., 1, *a,* but the question remains, why certain forms have been unable to go as far as others.

In part, I believe, this may be explained by the ecological preferences of the single species, and a comparison of a few of them will show what I mean. *Elliptio complanatus* is ubiquitous, and is able to live under a great variety of environmental conditions. It consequently had the best chance to spread north, and actually has the widest range of all. *Elliptio fisherianus* is a typical lowland species, and it has used the easy way over the coastal plain, and has succeeded in going farther north than the two allied species, *E. productus* and *lanceolatus,* which, as far as I can judge, are rather upland species, which could not avail themselves so much of the opportunities offered by the lowlands; they very likely depended more on stream capture within the mountains, which naturally was a slower and more difficult way of dispersal. Probably this holds good also in the cases of *Cambarus blandingi* and *C. acuminatus;* the former is a lowland species and has reached farther north than the latter, which seems to be an upland species.

This, however, is only a suggestion. Our knowledge of the actual distribution, and also of the ecological habits of these forms is not satisfactory enough to draw positive conclusions.

It is also possible, that the special history of these forms, chiefly with regard to their geological age, plays a part in this, and it might be that the oldest forms had the best chance to obtain the widest range. This might be correct in the case of *Elliptio complanatus,* while a rather recent type, *Eurynia constricta,* has stopped rather far south. But this surely is no general explanation, as is seen in the case of *Lexingtonia subplana,* a primitive type, which did not go farther north than *Eurynia constricta.*

This question should be taken up in connection with a more detailed study of the origin and the distribution of the southern At-

lantic element, and this is a problem correlated with the Tennessee-Coosa problem, and the connection of the Tennessee fauna with the southern and southeastern drainage systems of the Appalachians. It can be solved only after much more extended investigations in the Gulf and Atlantic streams from Alabama to the Carolinas.

This much is sure, that the existence of this southern element in the Atlantic fauna is well established. Simpson (1893, p. 355) already has indicated it clearly, and that it probably is connected with the fauna of the interior basin around the southern extremity of the Appalachians (see also Ortmann, 1905, p. 124). This center forms part of Adams' (1902 and 1905) great southeastern center, but is probably a rather sharply separated, and rather old subdivision of it. It had, with regard to aquatic life, a northward route of dispersal, not only in Postglacial, but also in Preglacial times, on the Atlantic slope. This route has been admitted by Adams (1905) for land-forms, but has not been mentioned (*l. c.*, p. 63) for aquatic forms.

FACT II., 2, (b).

Another element of the Atlantic fauna seems to have its center in the *north* (from Pennsylvania and New Jersey northward). The following *Najades* belong here: *Anodonta cataracta, Anodonta implicata, Alasmidonta varicosa, Lampsilis radiata, Lampsilis cariosa, Lampsilis ochracea,*[16] and the crayfish: *Cambarus limosus.* All these forms have in common, that they are most abundant northward, and advance southward either not at all (*Anodonta implicata*), or chiefly on the coastal plain. Only *Alasmidonta varicosa* seems to be more universal in its distribution on the Atlantic side. *Lampsilis ochracea* is a form of the lowlands (estuaries). *Lampsilis radiata* and *cariosa,* and apparently also *Anodonta cataracta* have a rather wide distribution in Pennsylvania, but southward they seem to occupy only a narrow belt on the coastal plain. The same is true of *Cambarus limosus.* However, our knowledge of the distribution of these forms in the lowlands of Virginia, and southward, is rather unsatisfactory, but the fact is undeniable that, while these

[16] *Margaritana margaritifera* and *Eurynia nasuta* resemble these to a degree, but, as we shall see below, are peculiar in other respects.

latter three forms are found in Pennsylvania way up into the mountain region in the Susquehanna, they are missing west of Blue Ridge in the Potomac,[17] James, and Roanoke. This fact, that the southward range of some of these forms falls largely within the coastal plain, where there were special advantages for migration, is corroborative evidence for their northern origin: they were first and originally present in the northern section of the Atlantic slope, where they had, in consequence of the longer time elapsed, a better chance to spread upstream.

I have treated of the origin of the distribution of a member of this northern fauna, *Cambarus limosus,* in a former publication (Ortmann, 1906, p. 428 ff.). I have pointed out, that this species is well marked, but possesses allied forms in the interior basin, and I have not the slightest doubt that the *Najades* enumerated above fall under the same head, and that the origin of their distribution is to be explained in a similar way. Also these *Najades* are well defined species, but possess allied representatives in the interior basin (see above p. 325).

According to the theory advanced for *Cambarus limosus,* these *Najades* came around the northern end of the Appalachians, in Preglacial times, by way of the Erigan River, which flew in the general direction of the present St. Lawrence. This river received the ancestral forms of these species from the interior basin (more especially from the lower Ohio and Tennessee drainage) in some way, which is at present not fully understood. But there is no serious obstacle to the assumption of this possibility on account of the probable numerous changes of the drainage in these parts. Having once reached the Atlantic coastal plain at the mouth of the Erigan River (region of St. Lawrence Gulf and New Foundland), there was no barrier to their farther dispersal southward, chiefly since the coastal plain, as we know, extended at certain times further seaward. This dispersal was first along the coast, but several of these forms migrated thence upstream in the various rivers of the Atlantic side.

[17] *C. limosus* is found here and there in the upper Potomac, but it probably reached these parts only recently by the aid of the Chesapeake-Ohio Canal.

The southward migration was unequal, but the causes of this are not very clear, but might be compared with the similar phenomenon in the case of the southern elements.

When the Glacial period set in, the ice coming from the north separated the eastern range of these forms from that on the western side. Habitudinal segregation was thus effected, and this induced differentiation into species. The final consequence is, that the Atlantic forms developed into well marked species, which have a rather young age (Glacial), and still are closely allied to corresponding forms in the interior basin. In Postglacial times, after the ice had disappeared, a reaction, a northward migration set in, and these species reoccupied a good deal of the territory lost in Glacial times. In this advance they were accompanied by certain southern types, which also invaded the glaciated area (*Elliptio complanatus, Alasmidonta undulata*).

Thus the origin and the history of this part of the Atlantic fauna appears rather clear. The most interesting fact is, that the case of *Cambarus limosus* has a number of parallel cases among the *Najades*. This element in the Atlantic Najad-fauna, however, has been recognized already by Simpson (1896*b*, p. 337), who also explains its origin by migration around the northern end of the Appalachians.

Considering the two elements together, the northern and the southern, and the fact that the species belonging to them migrated to various extents south or north, we obtain a satisfactory explanation of the fact, mentioned above (p. 315, 318), that the Susquehanna, and also the Potomac, fall short, in the number of species, of the rivers both to the north (Delaware) and south (James). Certain forms of the northern fauna have not gone south beyond the Delaware, and certain southern forms have not gone north beyond the James, and this leaves a balance against the intermediate systems of the Susquehanna and Potomac. In the Susquehanna, this shortcoming has been in part supplemented by an indigenous form (*Alasmidonta marginata susquehannæ*), and in the Potomac by a southern form (*Elliptio productus*). This peculiar condition is a point which very strongly speaks for our assumption of two distributional centers in the Atlantic fauna, a northern and a southern.

Fact II., 2, (c)

There is a third group of forms among the Atlantic fauna, which have for a common character the fact that they are *conspecific or extremely closely allied to western forms,* and which show in their distribution certain peculiar, but not quite uniform conditions. We have seen (under I., 2, *c,* p. 339, 357) that the corresponding western forms are in part characteristic for the mountain streams tributary to the Monongahela and Kanawha, so that there is the appearance, as if certain species had crossed the divide of the Allegheny Mountains. It remains to be investigated, whether such a crossing of the divide should be admitted, and what the means were, by which this was accomplished.

Certain cases, however, should be dismissed[18] from the beginning, namely first of all those, where passive migration by *transport* is probable or possible. The *Sphaeriidæ* belong here, and also *Campeloma decisum.* Here the whole character of the distribution is such, that it does not appear to follow drainage systems at all, but goes across country, suggesting exceptional means of dispersal, such as transportation by birds etc.

In other cases, *active migration* across divides is possible and probable: this concerns chiefly, as I have pointed out in a previous paper (Ortmann, 1906, p. 448), the crayfish *Cambarus bartoni.* This species, as well as the *Sphæriididæ* and *Campeloma decisum,* has a rather universal distribution east and west of the divide.

And further, I shall disregard here *Cambarus spinosus* and *acuminatus,* as belonging to the southern Appalachians, as far as it concerns the distribution on both sides of the divide, and also *Eurynia constricta* and *vanuxemensis* fall into the same class.

Thus there remain the following forms to be discussed here.

1. *Strophitus edentulus.*
2. *Alasmidonta marginata* and *marg. susquehannae.*
3. *Symphynota tappaniana.*

[18] Two very recent cases, *Cambarus obscurus* and *Lampsilis ventricosa* (*cohongoronta*), in the upper Potomac must be entirely disregarded, for here artificial, although accidental and unintentional, transplantation has been effected by human agency (see Ortmann, 1912*b*).

4. *Anculosa dilatata* and *carinata.*
5. *Cambarus longulus.*

The peculiarities of distribution in each of these cases have been shortly characterized above (p. 357) for the western side of the mountains, and it will be remembered that none of them are fully alike in all particulars, although resembling each other to a degree. This is also so on the eastern side. Thus it is best to take them up one by one.

Strophitus edentulus.

This species has a rather general distribution, but it is peculiar in so far as it is one of the two species of Najades which alone are found in the mountain-tributaries of the Monongahela (Youghiogheny and Tygart), while it is missing in the upper Kanawha region.[19] This forbids it to place this species simply with those which (like the *Sphæriidæ* and *Campeloma decisum*) have a universal distribution east and west of the divide. Indeed, the general distribution of *Strophitus,* for instance in Pennsylvania, might suggest that this form has exceptional means of dispersal, and might be transported from one drainage into another.[20] But its absence in the New River system speaks against this, for we cannot imagine that any means (birds for instance), which would have been able to carry this species across divides, should have carefully avoided the New River system.

Strophitus edentulus is a form eminently characteristic for small streams, and is rare or missing in large rivers. In the upper Alle-

[19] This negative statement might be doubted. But at the four localities, where I collected Najades (Ronceverte in Greenbrier River; Hinton and Pearisburg in New River; Wytheville in Reed Creek), shells were abundant, and in every case *I hunted for this species,* examining carefully also dead shells lying around; but no trace of *Strophitus* was discovered.

[20] In order to bring out all facts, which possibly might have a bearing upon this question, it should be mentioned, that Lefevre and Curtis (Science, 33, 1911, p. 863, and *Bull. Bur. Fish.,* 30 (for 1910). 1912, p. 171) have recently discovered a remarkable circumstance in the life-history of this species, different from all other known Najades: the larvae (glochidia) of *Strophitus* undergo their metamorphosis without a parasitic stage on fishes. For the present, however, I could not tell how this could favor passive transport of the young shell. But the fact should be kept in mind.

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gheny drainage it goes way up into the headwaters:[21] it is in the upper Youghiogheny and in the upper Tygart and Buckhannon rivers. Thus it closely approaches the divide in the whole northern section of the upper Ohio drainage. On the eastern side, it is also found close up to the divide in the Susquehanna, Potomac, James, and Roanoke drainages.[22] The eastern and western ranges are consequently in rather close contact along the northern part of the Alleghenian divide, from the uppermost Allegheny River to the region of the headwaters of the Monongahela, Potomac and James. But the close approach is most marked in central Pennsylvania, in Cambria, Indiana, and Westmoreland counties. Here this species is common in all small streams running east and west from the divide, and, for instance, the locality in Cush-Cushion Creek, belonging to the Susquehanna, is not more than twenty or twenty-five miles from the nearest localities in the Allegheny drainage (Creekside, Homer, Goodville).

This is just in the region where the Susquehanna drainage has largely encroached upon the drainage of the Allegheny River, and where stream capture has taken place. Although Davis (1889, p. 248) believes that this was accomplished chiefly in Pretertiary times, there is no objection to the assumption that to a lesser degree this process continued in the headwaters also during the Tertiary, in fact, that it is going on at present. If this is admitted, there is no difficulty in imagining that with the waters part of the fauna of the western streams was taken over into the eastern drainage, and since *Strophitus* inhabits these smaller western streams, it might thus have crossed the divide, in this region, *by the help of stream capture.*

[21] Potato Cr., Smethport, McKean Co.; Little Mahoning Cr., Goodville, Indiana Co.; Crooked Cr., Creekside, Indiana Co.; Yellow Cr., Homer, Indiana Co.; Blacklegs Cr., Saltsburg, Indiana Co.; Beaver Run, Delmont, Westmoreland Co.; Loyalhanna Riv., Ligonier, Westmoreland Co.; Quemahoning Cr., Stanton's Mill, Somerset Co.; all in Pa.

[22] For instance: in the system of the Susquehanna: Cush-Cushion Cr., Greene Twp., Indiana Co.; Chest Cr., Patton, Cambria Co.; Swartz Run, Ashville, Cambria Co.; Beaver Dam Cr., Flinton, Cambria Co.; Raystown Branch Juniata Riv., Everett and Mt. Dallas, Bedford Co.; all in Pa.; South Branch Potomac Riv., Romney, Hampshire Co., W. Va.; James drainage: Calf Pasture Riv., Goshen, Rockbridge Co., Va.; Roanoke drainage: Mason Cr., Salem, Roanoke Co., Va.

Of course, this presupposes that the original home of this form was in the interior drainage basin. But I hardly think that this could have been otherwise, on account of the tremenduous range of *Strophitus edentulus* in the west, and we have seen that the Atlantic slope probably never has been an important center of development. *Strophitus* differs from all the other elements of the Atlantic fauna (discussed so far) by the fact that the identical species is found on either side of the mountains. Thus it is improbable that it had a similar history to that of the other forms (the northern and southern elements) of the Atlantic fauna, and we are forced to assume a special explanation of its distribution. I think, that the evidence introduced above favors the theory, that it actually crossed the divide by the help of stream capture, or in other words, by the shifting of the divide, and that this probably took place in the region of the headwaters of the West Branch Susquehanna. It might have happened elsewhere; it might have happened repeatedly: but the region indicated is the most likely. After having once (or repeatedly) crossed, this species spread over the Atlantic slope, both north and south, and occupies now the whole of it, from Virginia to New England (exact data from Virginia southward are lacking). This of course, was accomplished by the same means as in the other members of the Atlantic fauna, and it is not astonishing since this species is not only upon the Piedmont Plateau, but also on the Coastal Plain.[23]

Further details cannot be given, and chiefly it is impossible to fix the geological time when *Strophitus* crossed the mountains. As has been said, possibly this happened repeatedly, presumably in the Tertiary, and may have happened even later.[24] More information as to its southern range may furnish additional evidence, and confirm the view that the crossing of the divide was effected in the northern section of the Alleghenies, and not in the south. At pres-

[23] I found it in Delaware River, Penns Manor, Bucks Co., Pa. Its distribution upon the Coastal Plain is yet incompletely known, but it seems to be represented there at least by a local (or ecological?) form, *Strophitus undulatus*.

[24] At present, this species has a continuous range from West to East in the state of New York, and this, of course, belongs to the Postglacial time.

ent, the absence of it in the New River system is the most important fact which speaks for the assumption made above.

Alasmidonta marginata and Alasmidonta marginata susquehannæ.

The typical western *Alasmidonta marginata* has a wide distribution in the interior basin, and in the Allegheny Mountains it goes up into the headwaters of the Holston, Clinch, into New River, and into the uppermost Allegheny River, but it is not found in the headwaters of the mountain-tributaries of the Monongahela (although it is immediately below the canyon in the Cheat). In the upper Allegheny, it goes, like *Strophitus,* into very small streams,[25] and it is in general a species characteristic for smaller streams, avoiding large rivers.

On the Atlantic side, it is represented by two forms. The one is *Alasmidonta varicosa,* a closely allied, but nevertheless sharply distinct species, which has been discussed above (p. 363 f.) together with those forms constituting the northern element in the Atlantic fauna, which migrated, in Preglacial times, around the northern end of the Appalachian chain.

But there is a second representative on the Atlantic side, which has been hitherto overlooked, and which I have called *Alasmidonta marginata susquehannæ,* which stands much closer to the western form, in fact, is very hard to distinguish from it. This form is restricted to the Susquehanna drainage in Pennsylvania and New York, and it is found frequently associated with *A. varicosa,* but is always perfectly distinct from it.

It seems, according to the material at hand, that *Alasmidonta marginata susquehannæ* has its metropolis in the Juniata River and the part of the Susquehanna in central Pennsylvania, which is below the junction of the west and north branches. It has not been found in the west branch and its tributaries (although *Al. varicosa* is there), but we should consider that the fauna of this branch is poorly known, and that it has been largely destroyed by pollution from mine waters.

[25] Allegheny River, Larabee, McKean Co.; Little Mahoning Creek, Goodville, Indiana Co.; Loyalhanna River, Ligonier, Westmoreland Co.; Quemahoning Creek, Stanton's Mill, Somerset Co.; all in Pa.

In the localization of its eastern range, this form differs from *Strophitus*. But just this fact points to a connection across the divide with the western range of *Al. marginata*. This comes up, on the western side, close to the divide, and although the corresponding form is not known from the West Branch Susquehanna, the distribution on the eastern side suggests that it must have crossed the divide in this general region, presumably in consequence of stream capture. This is the more probable, since the western race of *Al. marginata* found in the headwaters of the Allegheny in Indiana, Westmoreland, and Somerset Cos., in Pa., approaches the Susquehanna-form much more closely than the typical *marginata,* as found, for instance, in the Beaver drainage.

This leads us to consider this as a parallel case to that of *Strophitus edentulus*. *Alasmidonta marginata* crossed the divide by similar means and in about the same region as *Strophitus;* but there is the difference that it did not spread beyond the Susquehanna drainage, This may be explained by the assumption that this crossing, in the case of *Alasmidonta,* falls into a later time.

Of course, this explanation is only tentative, but according to our present knowledge, it is the only possible one. The fact of the restriction of *Al. marginata susquehannæ* to the Susquehanna drainage is of the greatest weight for our argument, since we cannot imagine that this form reached its present area by any other way.

Symphynota tappaniana.

Up to shortly ago, this species was known only from the Atlantic slope, where it has a wide distribution from New England to Virginia (allied species are in North and South Carolina). On account of its relation to the western *S. compressa,* it appeared to fall into the group which has been designated as the northern element in the Atlantic fauna (indeed, Simpson, 1896*b,* places it there). But after I discovered that this species is also found in the western drainage, but only in the upper Kanawha system (Greenbrier and New rivers), where it is extremely abundant, in fact the prevailing form of Najad-life, the history of it must be different.

Its general distribution in the east, and its localization in the west, might suggest that we have here a case like that of *Alasmi-*

donta marginata, but *reversed,* and that the original range was on the east side, and that the upper Kanawha received it from the east, probably by stream capture, since transport over land is not very likely on account of the improbability that birds (or other creatures) carried this species only into the Kanawha, and refused to do so into other western streams.[26]

But as we have seen above, it is not probable that the upper Kanawha has captured any streams of the eastern drainage, but rather the reverse is true (above, p. 346 f.). The present course of New River represents most nearly the ancient drainage features, while the eastern streams (Roanoke, James and possibly also Potomac) have captured sections of the old New River and Greenbrier system. New River runs within the mountains on a distinctly higher level than most of the other streams which have cut much more deeply into the Cretaceous base-level, and thus had a better chance to capture parts of New River, than vice versa (see Pl. XIV., fig. 1).

This induces us to assume that *Symphynota tappaniana* originally was a local form of the New River drainage, developed probably out of the western *S. compressa* as an ecological mountain-form. In this case it is strange that the range of *S. compressa* does not come very near to that of *S. tappaniana,* but this may be due to a subsequent restriction of the range of *S. compressa.*[27]

[26] There is, however, one fact in favor of this assumption. *S. tappaniana* is one of the few cases of hermaphroditism known in Najades. If we grant, that in rare cases, specimens have been transported, we must admit the possibility that a new stream might have become stocked with this species, by the transplantation of a single individual. But then again, we do not know, whether self-fertilization occurs here. I mention this here, to bring out all possible arguments.

[27] The nearest place known to me for *S. compressa,* is Little Kanawha River, where it is very rare, and also this locality is isolated. Forms like *S. compressa* and *tappaniana* seem to be absent in the upper Tennessee drainage, but in the latter is *Symphynota holstonia* (which is *not* an *Alasmidonta*), and a very doubtful, incompletely known species, *S. quadrata* (Lea), which has a certain external resemblance to *S. tappaniana,* but may be anything. *S. holstonia* is surely *not* closely related to *S. tappaniana,* for it has no lateral hinge-teeth. It remains to be seen, whether there are any related forms in the upper Tennessee, which, when present, might suggest, that New River received its species from the Tennessee.

After *S. tappaniana* had reached the James drainage (it has not been found in the Roanoke, but only the headwaters of this are known), it had a chance to spread on the Atlantic side and to attain its present wide range, exactly as the majority of the Atlantic forms, favored by the same causes. It always remains a small-creek-form, but just in these small creeks the best opportunities were given to cross from one system into the other.

Anculosa dilatata and carinata.

Anculosa carinata is the Atlantic form and is known to me from the Roanoke to the Susquehanna, where it goes up into New York state. In this restriction (not being found in the Delaware and beyond) it is different from *Strophitus* and *Symphynota tappaniana,* which go to New England. West of the divide we have *Anculosa dilatata,* first of all in the same region where *Symphynota tappaniana* is found (Greenbrier and New rivers); but in addition it is also in the upper Monongahela drainage, in Tygart and Cheat rivers; in the latter it goes down below the canyon, as far as Cheat Haven, Fayette Co., Pa., and further it is found in West Fork River. Remarkably enough, it is absolutely absent in the upper Youghiogheny, although the conditions appear favorable for it.

With exception of these localities in the Monongahela drainage, the distribution fairly well agrees with that of *Symphynota tappaniana,* and we won't make a mistake if we advance the same explanation for it: stream capture on the part of certain Atlantic streams (Roanoke and James), which robbed the water and the fauna of certain parts of the old New River drainage. Thus only the presence of this form in the Tygart and Cheat needs explanation; into West Fork River it undoubtedly got from the Tygart.

The headwaters of these rivers interlock in a very complex way in Pocahontas and Randolph Cos., W. Va. (see Pl. XII.), and there is no objection on general principles to assume that there has been intercommunication of these rivers by stream capture. But conditions are rather obscure in this region and have been so little investigated from a physiographical standpoint that it is practically impossible to draw any positive conclusions as to the history of the development of the headwaters of these systems.

But it is highly interesting to notice that the distribution of *Anculosa dilatata* in the Greenbrier on one side, and in the Tygart and Cheat on the other, points to stream capture in this region, and the theory is suggested that the Monongahela drainage encroached upon and robbed the Greenbrier drainage. The opposite way is not possible on account of the limitation of this form northward, and this also speaks against the possibility of passive transport. If this assumption is correct, it also explains the fact that the Youghiogheny, which also heads in the same general region, did not receive this species. The upper Youghiogheny flows in a high synclinal valley, is more nearly an old consequent river than, for instance, the upper Cheat, which has cut down way below the level of the upper Youghiogheny. Thus it is impossible that the latter ever robbed the Cheat, capturing its fauna; rather the opposite has happened, and probably is happening now.

The Atlantic form, *Anculosa carinata,* after having reached the Roanoke and James, and after having become established on the eastern side, had the same tendency to spread as the rest of the Atlantic forms. But it did not go so far as many others, reaching only the Susquehanna drainage. In this case northward migration probably was due to the crossing over divides (by stream capture) in the mountain region. *Anculosa* is a shell characteristic for rough water in mountain streams and goes possibly farther up than any other of the forms discussed here. In the lowlands, it has never been found, and it is also less frequent in the Piedmont section of the streams, although present there. Thus its migration very likely took place chiefly within the mountains, and I think that its limited range northward is due to this fact.

The genus *Anculosa* is represented in the uppermost Tennessee drainage by the species *Anculosa gibbosa,* which is to a certain degree related to the *dilatata-carinata*-group. In fact, the Tennessee drainage is the only other region where relations of this are found. This makes it clear that New River must have received its *Anculosa*-stock from the upper Tennessee. It is hard to say how this was accomplished. We have seen (p. 352 f.) that stream capture was rare in this region; at any rate, if there was any, it was rather in the

opposite direction. Nevertheless, there might have been cases where in the headwater region smaller streams have been deflected from the Holston or Clinch to the New River, and since *Anculosa* is an abundant small-creek-type, it might thus have managed to get across. But in this case also transportation is to be considered as a possible means, since many of the headwaters originate in the same longitudinal valleys, and come very close to each other without sharp barriers between them. But the fact that the species in the two systems are sharply distinct speaks against this, for if transport had been possible once, it should have been possible repeatedly, which would have prevented specific isolation.

Cambarus longulus.

The distribution of this species again agrees, in a general way, with that of *Symphynota tappaniana* and of *Anculosa,* but is rather more restricted on either side.

It is extremely common in the whole Greenbrier and New River drainages. It is also found in the upper Tennessee. On the eastern side it is common in the James drainage, but has not been found in the Roanoke, and besides, it has been reported from the uppermost Shenandoah (Waynesboro, Augusta Co., Va.). Farther north, chiefly in the rest of the Potomac drainage, it is positively absent, and also on the west side it does not go into the upper Monongahela system (as *Anculosa* does).

Its presence in New River and Tennessee in forms which are specifically identical shows a closer connection of these two faunas than in any of the previous cases. We have seen that in *Cambarus bartoni,* a closely allied species, general distribution is very likely due to active or passive migration across divides. This might be true also here. But *Cambarus longulus* differs from *C. bartoni* in its ecological habits, inhabiting preferably larger mountain streams, and not the smallest headwaters or even springs, as *C. bartoni* does. For all practical purposes we may compare *C. longulus* with *Anculosa,* and whatever the means were which permitted *Anculosa* to get from the Tennessee into the New River, might have worked as well in the case of this crayfish. Having reached the New and Green-

brier, it did not go beyond this drainage on the western side and did not reach upper Tygart and Cheat as *Anculosa* did. The reasons for this as well as for the fact that it did not become specifically distinct in New River are unknown for the present, but probably they are to be found in a difference of the time of migration from that of *Anculosa*.

From New River, *C. longulus* got into James River by the same means as *Symphynota tappaniana* and *Anculosa, i. e.,* by stream capture. It did not get out of this drainage except at one place, in the uppermost Shenandoah. This is probably to be connected with the stream piracy committed by the Shenandoah all along its present valley (see above, p. 347). Just at Waynesboro there is a wind gap in the Blue Ridge, Rockfish Gap, which undoubtedly once served as an outlet for a tributary of the James River (Rockfish Creek or Mechum River), which was beheaded by the Shenandoah exactly as was Beaverdam Creek at Snickers Gap (Davis, 1891, p. 576).

The question remains, why *C. longulus* did not spread over the rest of the Shenandoah and Potomac drainage. This may be due to ecological causes. The species may not find farther down in the Shenandoah a congenial environment. Where I found *C. longulus* the water was always rough and full of rocks, and the lower Shenandoah, although by no means a sluggish river, has considerable quiet stretches. I also found this species generally at elevations higher than the Shenandoah in the average. This would correspond to a degree to the conditions seen in *C. bartoni,* which is also a species avoiding larger streams and quiet water.

Taking these last three cases together, *Symphynota tappaniana, Anculosa,* and *Cambarus longulus,* it is seen that, although they differ in particulars, they fall under one general head, and that very likely similar causes were working to effect their distribution. Disregarding *Strophitus* and *Alasmidonta,* which probably crossed the divide farther north, they are the only cases where freshwater forms seem to have crossed the Allegheny divide in its central parts, probably by the help of stream capture.

The total number of such cases is very small compared with the numerous cases which follow the general rule, that the Allegheny

Mountains have formed and are forming a sharp barrier between the western and eastern fauna. But this is exactly what was to be expected, for the distribution of freshwater animals is primarily governed by the conformation of the drainage systems and their boundaries, provided there are no exceptional means of dispersal which permit a transport or migration over land.

Special Cases.

So far we have attempted to explain those cases which submitted to a classification such as has been given above (Chapter 4, pp. 338–341). But perusing the end of Chapter 2 (pp. 324, 325), we see that not all forms have been treated and that there are among the *Najades* at least three others which show special features. These are: *Margaritana margaritifera, Eurynia constricta, Eurynia nasuta.*

We may pass over *Eurynia constricta* with a few words. This species belongs undoubtedly to the southern element in the Atlantic fauna, and has been treated with it above. The peculiarity in this case is that it has an extremely closely allied species in the headwaters of the Holston (and elsewhere in the Tennessee drainage). It might be possible that here we have evidence of a direct crossing from the Holston into the Atlantic drainage. But as far as we know, the two species do not come in close contact with each other in the region investigated, and if there is any contact it is somewhere else, probably in the southern Appalachians, and this case thus would belong to the Tennessee-Coosa problem. It should be added that probably also two crayfishes fall into the same class, *Cambarus acuminatus* and *C. spinosus.*

The other two cases must be treated separately, each forming a class by itself.

Margaritana margaritifera.

In our region this species is found exclusively in the upper Schuylkill drainage in Pennsylvania (Schuylkill Co.). This is the only locality known outside (to the south) of the terminal Moraine. Farther to the northeast, within the Glacial area, in New York and New England, and all the way to New Foundland, this species is rather abundant. In addition, it is found (in a somewhat different

form) in northwestern North America and in absolutely the same form in Iceland and parts of Europe and Asia. The distributional facts have been summarized by Walker (1910), and as to the origin of the distribution he draws the conclusion (*l. c.*, p. 139) that the presence of this species in northeastern North America is best explained by the assumption that it immigrated, probably in late Tertiary times, from Europe by a land-bridge over Iceland and Greenland.

I accept this fully. Also the idea of Walker, that the Glacial epoch restricted the range of this species, must be accepted. In fact, we are to regard the present station in Pennsylvania as *the last remnant of the Glacial refugium* of this species, just in front of the terminal Moraine. Here it survived and the present distribution is largely a Postglacial re-occupation of lost territory,[28] and in this it fully agrees with the other Atlantic forms, chiefly the northern element. It differs, however, from the latter in its ecological preferences: *Margaritana* is a form of cold water and is averse to limestone.

Thus it is evident that *Margaritana* is a stranger among the other *Najades* of the Atlantic side, in fact, it is an element of the North American fauna which stands by itself and has been subject to entirely different laws in its distribution. It is true, there is a shell in the interior basin which is allied to it, but only remotely so, belonging to another genus: *Cumberlandia monodonta* (Say). Another one is *Margaritana hembeli* (Conrad) from southern Alabama and Louisiana.[29] Both of these do not seem to have any direct genetic connection with *M. margaritifera* and are probably relics of a former more general distribution of this most primitive and archaic group of *Najades,* undoubtedly reaching back in their history far beyond the other *Najades* and far into Mesozoic times.

Eurynia nasuta.

On the Atlantic side this species is found from the Delaware

[28] It is doubtful, whether all of the present range was regained from this Pennsylvanian stock; it is quite possible, that there were other refugia, situated on the former seaward extension of the present coast. The Pennsylvanian refugium is the only one, which has been positively ascertained.

[29] The so called *Margaritana decumbens* (Lea) of Alabama is an extremely doubtful form in every respect (see Walker, *l. c.*, p. 128).

River estuary northward, and goes probably a little farther south on the Coastal Plain into Virginia. In this distribution it would agree very well with the northern stock of the Atlantic fauna. But it differs from the members belonging to this in that it has no representative species in the upper Ohio basin. However, it is found on the western side of the Alleghenies and is widely distributed in the lake drainage, chiefly in Lake Erie and the state of Michigan, and it is absolutely the same form that is found there. The fact is that these ranges are not disconnected, but appear to be rather continuous across the state of New York and the known localities follow in a general way the line of the present Erie canal from Buffalo to the Hudson River at Albany. This region lies outside the scope of the present paper, but it should be mentioned here that there are other western species of *Najades* which follow the same line of dispersal eastward from the St. Lawrence drainage to Hudson River. It is very likely that *Eurynia nasuta* belongs to this group, and it probably is the one of them which has reached in modern times the widest dispersal upon the Atlantic side. Its western origin is confirmed by the fact that the only species allied to it, *Eurynia subrostrata* (Say), is western and is found in the central and western parts of the interior basin in large, quiet rivers, ponds and lakes, avoiding rough water and strong current. For this reason, probably, it is not found in the upper Ohio drainage. This species has crossed somewhere in the region from northern Illinois to northern Ohio into the lake drainage, developed there into the species *nasuta*, which then spread eastward, following the quiet waters of the lakes and those of the canal till it reached the estuary of the Hudson. Thence it had no difficulty to spread farther over the Coastal Plain and reached across New Jersey[30] the lower Delaware, and even beyond. Also on the Atlantic side it preserves its preference for lakes, estuaries, canals, etc., that is to say, for quiet water.

We thus are to regard *Eurynia nasuta* as a quite recent immigrant in the Atlantic drainage, belonging surely to the Postglacial time, and this immigration might have been completed even by the

[30] It is present, for instance, in the Delaware-Raritan canal at Princeton, N. J.

help of the modern, artificial canals. But, of course, it is difficult to decide positively whether canals have played a necessary part in this dispersal. This question should be investigated in connection with the other western forms, which have taken the route of the Erie canal; but this is not our present object.

The above studies would be more complete if the conclusions were supported by *paleontological evidence;* if we had fossil remnants of *Najades* or other aquatic creatures which would give us an idea as to the faunas of the two watersheds in the past, chiefly during Tertiary times. It is very much to be regretted that practically nothing is known in this line.

There is indeed a famous locality, Fish House, Camden Co., New Jersey, opposite Philadelphia, which has yielded fossil *Najades,* probably belonging to the Glacial time. These shells have been described and discussed by Lea and chiefly by Whitfield (Mon. U. S. Geol. Surv., 9, 1885), and their geological age has been ascertained by Woolman (Ann. Rep. Geol. Surv. N. J. (for 1896), 1897, p. 201 ff.), Pilsbry (*Pr. Ac. Philad.,* 1896, p. 567) and Simpson (Pr. U. S. Mus., 1895, p. 338). But for the present time these fossils are absolutely useless, because western affinities have been maintained for these species, which surely do not exist. The species have been identified mainly from casts, and Lea as well as Whitfield have indicated, by the names given to them, their supposed affinities to western species. I have taken the trouble of making plaster casts of the inside of specimens of the living species with which they have been correlated, and practically in all cases it became evident at a glance that there was no similarity at all.

But this should be the subject of a special paper. It suffices here to make the statement, first, that the number of species described from this deposit (about a dozen) should be reduced to not more than three or four, and second, that there is not a single one which has distinct and unmistakable affinities to any typical western species.

SUMMARY OF CONCLUSIONS.

1. I think that the present studies have demonstrated the fundamental fact, *that certain freshwater animals are apt to furnish important evidence for past conditions of drainage by their present distribution,* while others are not. The most important of the former are the *Najades.* There are many cases (not only in our region) where indentical or closely allied species are found in different drainage systems which have at present no direct water connection. Such cases are generally restricted to *limited, well-defined regions.*

In our region we have seen that such cases exist in the mountains in the section which has the upper New River for its center; but similar instances are known in Pennsylvania, in the headwaters of the Susquehanna.

This *localisation* is the most important evidence against the assumption that passive transport over land has played a part in these cases: if this was possible at all, or if it was a factor to be considered, evidence for this should be general. But just where we might expect that transport should have worked by all means, there is no evidence whatever for it. This is most especially true in the case of the divide between the upper Tennessee drainage and that of New River. If *Najades* should be able to cross divides by being transported, it should have happened just here. Also the general condition of the eastern and western fauna, its dissimilarity, shows that *Najades* were not transported across the mountains.

Very likely the freshwater snails of the family *Pleuroceridæ* submit to the same general law as the *Najades* and are important for the study of the old drainage features. But they should be further studied, chiefly with regard to their actual distribution, their systematics and relationships. Finally, some crayfishes of the genus *Cambarus* are extremely valuable in this respect, but unfortunately their number is not great.

2. *The Allegheny system forms an old and very well-marked boundary between aquatic animals inhabiting the interior basin and the Atlantic slope.* This barrier may have been rendered insignifi-

cant at certain times in the past. But beginning with the Post-cretaceous elevation of the country and the subsequent rejuvenation of all drainage systems, this barrier has been emphasized again and persists to the present time.

3. *The uniformity of the fauna of the upper Ohio basin is a character acquired in Postglacial times,* and it has been shown that not only Big Sandy River, but also Licking River, and possibly also Kentucky River, belong to the upper Ohio basin, and not to the Cumberland-Tennessee drainage. In this case *zoögeographical evidence contributes to the solution of a question which has not been fully settled by physiographical methods.*

4. *On the western side we have remnants of an older (Preglacial) faunistic differentiation.* The most important division is the Tennessee-Cumberland fauna, of which, however, only a small part has been considered in the present paper, and which deserves more detailed study. Other remnants of what might be Preglacial faunas are possibly seen in the headwaters of the Monongahela and Kanawha rivers. But in these cases the physiographical development of these parts must be studied more closely before we can arrive at a final conclusion.

5. *The Atlantic fauna is a distinct fauna and the creation of two faunal provinces, Mississippian and Atlantic* (Simpson, 1900, p. 505), *is fully justified.* Nevertheless, the Atlantic fauna is a secondary one, derived originally from that of the interior basin, and its chief character consists in the absence of a great number of types of the interior basin.

6. *Within the Atlantic fauna we have to distinguish two main elements, a northern and a southern.* The northern came from the interior basin around the northern end of the Alleghenies; the southern came around the southern end. The former belongs to the Preglacial time, but is not very old, while in the latter there are some rather ancient elements, going back possibly to the earlier Tertiary, or even beyond. The southern element probably is closely connected with the Tennessee-Coosa problem.

7. *Along the Atlantic slope we have a dispersal line directed both north and south,* which has been clearly recognized, for land-forms,

by Adams (1902 and 1905). But this route was available *also for aquatic forms of life* and lies probably mainly upon the Coastal Plain, where barriers are largely removed by base-leveling. To a smaller degree stream piracy in the uplands may have played a part in the dispersal of the Atlantic forms.

8. *In the mountains we know a few cases which indicate crossing of the divide,* but compared with the mass of the fauna, these cases are very insignificant. However, they are zoögraphically of the greatest interest in so far as *they indicate probable cases of stream capture.* In order to properly understand these cases, the physiography of the region involved should be studied more closely.

9. *In addition, we have on the Atlantic side a few cases of abnormal distribution for which special explanations have been advanced.* One of them concerns a form, *Margaritana margaritifera,* which differs in the origin of its distribution entirely from all North American *Najades,*[31] and which is a stranger in our fauna. The other case, *Eurynia nasuta,* possibly is due to Postglacial migration from the St. Lawrence basin to the Atlantic slope, and may be in part quite recent.

10. *Further investigations* should be made primarily in the region of the southern Atlantic slope and in the southern Appalachians, and should be connected with the study of the Tennessee-Coosa problem from the zoögeographical side. In this region there are extremely interesting conditions, which, however, are very unsatisfactorily known, and have led Johnson (1905) to the erroneous assumption that the evidence taken from the *Najades* is unreliable with regard to the reconstruction of the old drainage systems.

In addition, other freshwater groups should be studied. In the present paper the *Najades* have furnished the chief evidence, but it has been shown that also certain *Gastropods* and the *Crayfishes* are or might be valuable; but there are surely other groups, chiefly the Fishes.

[31] At present, only a land snail, *Helix hortensis* Muell., falls under the same head.

PROC. AMER. PHIL. SOC. LII. 210 G, PRINTED JULY 18 1913.

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CARNEGIE MUSEUM,
PITTSBURGH, PA.,
April 18, 1913.

EXPLANATION OF PLATE XII.

MAP OF THE ALLEGHENY SYSTEM OF VIRGINIA, WEST VIRGINIA, MARYLAND AND PENNSYLVANIA.

The chief *Physiographical Divisions* are:

AP: Allegheny Plateau; *AM:* Allegheny Mountains; *AV:* Allegheny valley; *PP:* Piedmont Plateau; *CP:* Coastal Plain. They are marked off by heavy dotted lines. From the upper Clinch River to Covington, on Jackson River, runs another dotted line, which indicates the chief *fault* of this region, discussed in chapter 5, p. 345. The line of heavy dashes represents the *divide* between the Interior Basin drainage in the West, and that of the Atlantic Slope (including the St. Lawrence) in the East and North.

The following abbreviations for rivers and creeks have been used:

Upper Ohio and Allegheny drainage:

All = Allegheny River.
Bv = Beaver River.
Clar = Clarion River.
Con = Conemaugh River.
Cr = Crooked Creek.
Fr = French Creek.
Kis = Kiskiminetas River.
Loy = Loyalhanna River.
Mah = Mahoning Creek.
Po = Potato Creek.
Qu = Quemahoning Creek.
RB = Red Bank Creek.

Monongahela drainage:

Bl = Blackwater River.
Bu = Buckhannon River.
DF = Dry Fork.
SF = Shavers Fork.
Tyg = Tygart Valley River.
WF = West Fork River.

Tributaries of Ohio in West Virginia and Kentucky:

F = Fish Creek.
Fg = Fishing Creek.
Hg = Hughes River.
L. Fk = Levisa Fork of Big Sandy River.
L. Kan = Little Kanawha River.
M. I. = Middle Island Creek.

Delaware drainage:

Leh = Lehigh River.
Liz = Lizard Creek.
P = Princess Creek.

Susquehanna drainage:

C. C. = Cush Cushion Creek.
Ch = Chest Creek.
Cl = Clearfield Creek.
Coned = Conedoguinet Creek.
Conew = Conewago Creek.
N.B. = North Branch of Susquehanna.
Si = Sinnemahoning Creek.
Sw = Swatara Creek.
Ti = Tioga Creek.
W. B. = West Branch of Susquehanna.

Potomac drainage:

An = Antietam Creek.
Con = Conococheague Creek.
N. B. = North Branch Potomac River.
S. B. = South Branch Potomac River.
To = Tonoloway Creek.
W = Wills Creek.

James drainage:

N = North River (headwaters called: Calf Pasture River).
RF = Rockfish Creek.
Riv = Rivanna River.

Roanoke drainage:

N. F. = North Fork Roanoke River.

Holston drainage:

Holston = North Fork Holston River.
M. F. = Middle Fork Holston River.
S. F. = South Fork Holston River.

EXPLANATION OF PLATE XIII.

Profiles of Rivers.

Fig. 1. Profile up from Pittsburgh, Pa., along Allegheny River, Mahoning and Little Mahoning Creeks to Divide, and thence down along Cush Cushion Creek, West Branch Susquehanna, and Susquehanna River to Havre de Grace, Md. (sea level).

Between Curvensville and Keating the river has not been accurately surveyed.

Compiled from: U. S. Geol. Surv. Atlas Sheets, and Hoyt and Anderson, 1905, pl. 28 and 29.

Fig. 2. Profile from a little above McKeesport, Pa., up the Monongahela and its tributaries (Youghiogheny, Cheat and Shavers Fork, Tygart Valley River, West Fork River) to the Divide, and thence down the South and North Branch and the Potomac River, to Washington, D. C.

The sources of Shavers Fork and South Branch Potomac are about twenty miles apart. On account of the exaggerated vertical scale, the headwaters of all rivers appear much longer than they actually are.

Compiled from: U. S. Geol. Surv. Atlas Sheets, and Bolster, 1907, pl. 5 and 6.

EXPLANATION OF PLATE XIV.

Profiles of Rivers and Mountains.

Fig. 1. Profile from Charleston, W. Va., up the Kanawha, New and Greenbrier Rivers, to the Divide, and thence down the Jackson and North Rivers to Lynchburg, Va., on James River. Also the profile of the upper Roanoke is given and its location with reference to New River, and the old abandoned valley connecting the two. The upper parts of New River are only roughly sketched.

The sources of Greenbrier and Jackson Rivers are about fifteen miles apart.

Compiled from U. S. Geol. Surv. Atlas Sheets.

Fig. 2. Profile along the crest of the Allegheny Front, and the ranges farther south (Peters and East River Mountains), which form its continuation. The rivers and creeks at the eastern foot of the mountains are indicated by dotted lines. In the region of the B. & O. Tunnel exact data are missing. The two sections of the profile are connected at $x-y$. The range behind Dans Mountain is Savage and Backbone Mountain.

Compiled from U. S. Geol. Surv. Atlas Sheets.

Explanation of abbreviations:

Streams:

Cl = South Fork Clinch River.
St = Stony Creek.
Du = Dunlap Creek.
N. Fk. S. Br. Pot. = North Fork of South Branch Potomac.
N. Br. = North Branch Potomac.
Ray = Raystown Branch Juniata Riv.
Dun = Dunning Creek.
Fra. Jun. = Frankstown Branch Juniata River.
W. G. = Water Gaps (of New River, flowing West, and of Potomac, flowing East).

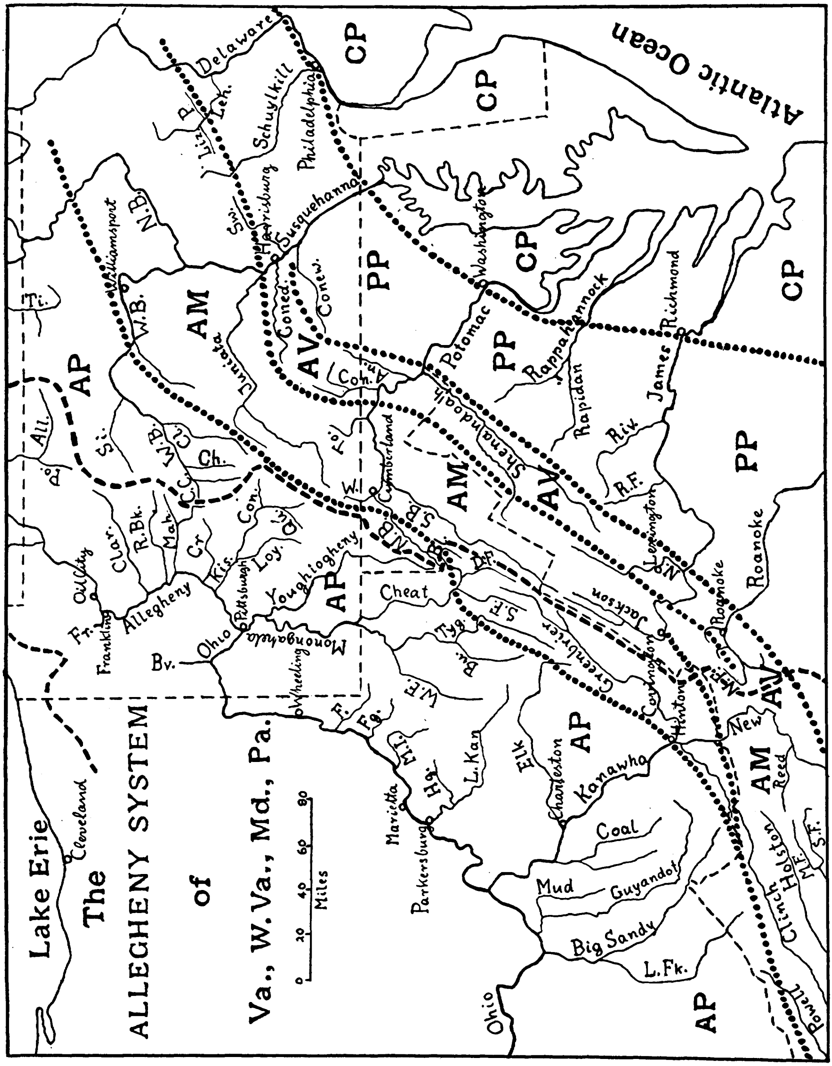
Towns:

Cov = Covington, Va.
Pet = Petersburg, W. Va.
Cumb = Cumberland, Md.
Holl = Hollidaysburg, Pa.

Tunnels:

C. & O. = Chesapeake and Ohio R. R.
B. & O. = Baltimore and Ohio R. R.
P. R. R. = Pennsylvania R. R.

It is believed that the depression in the region of the C. & O. Tunnel is a remnant of the Cretaceous Peneplain.


The
ALLEGHENY SYSTEM
of
Va., W. Va., Md., Pa.
0 20 40 60 80
Miles
Lake Erie
Cleveland
Atlantic Ocean
CP
PP
AM
AV
AP
Delaware
Schuylkill
Philadelphia
Susquehanna
Harrisburg
Williamsport
Juniata
Washington
Potomac
Rappahannock
Rapidan
Richmond
James
Riv.
R.F.
Shenandoah
Cumberland
Lexington
Roanoke
Jackson
Greenbrier
Covington
Hinton
New
Reed
Holston
Clinch
Powell
Kanawha
Charleston
Elk
Coal
Mud
Guyandot
Big Sandy
L.Fk.
Ohio
Parkersburg
Marietta
L.Kan
Wheeling
Monongahela
Pittsburgh
Youghiogheny
Cheat
Allegheny
Oil City
Franklin
Clar.
R.Bk.
Mah.
Kis.
Loy.
Con.
Ch.
Bv.
W.F.
Tyg.
S.F.

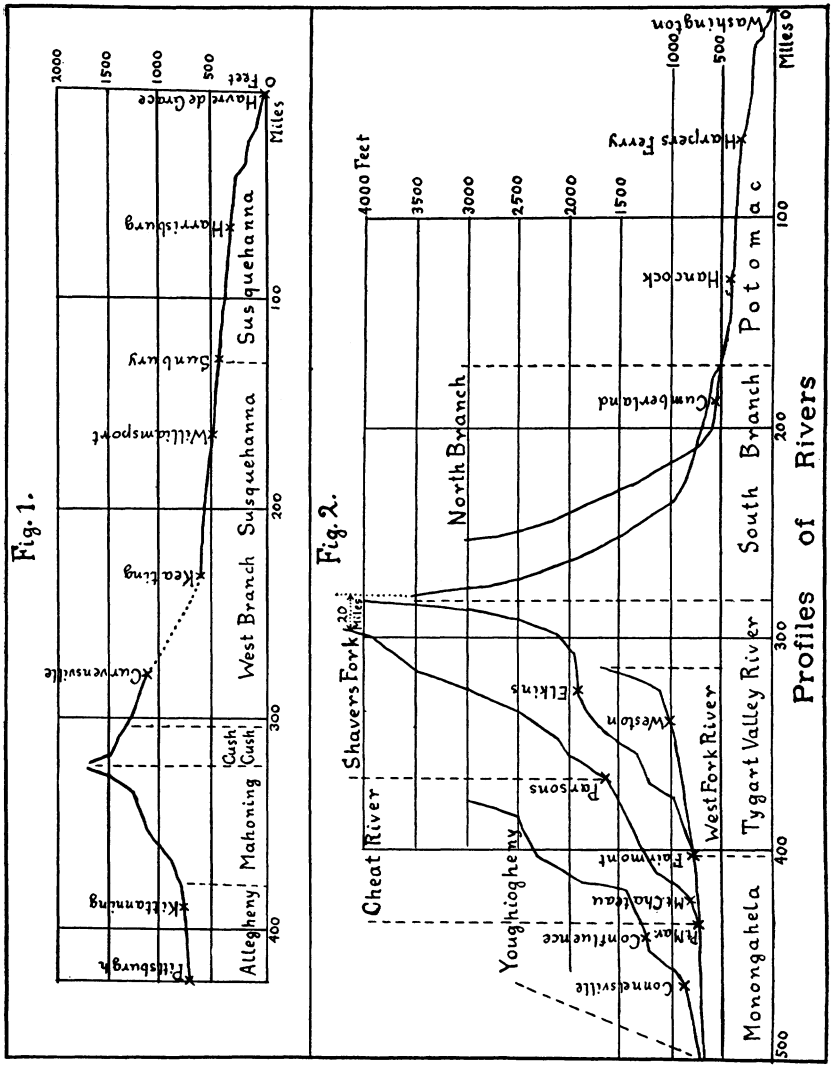
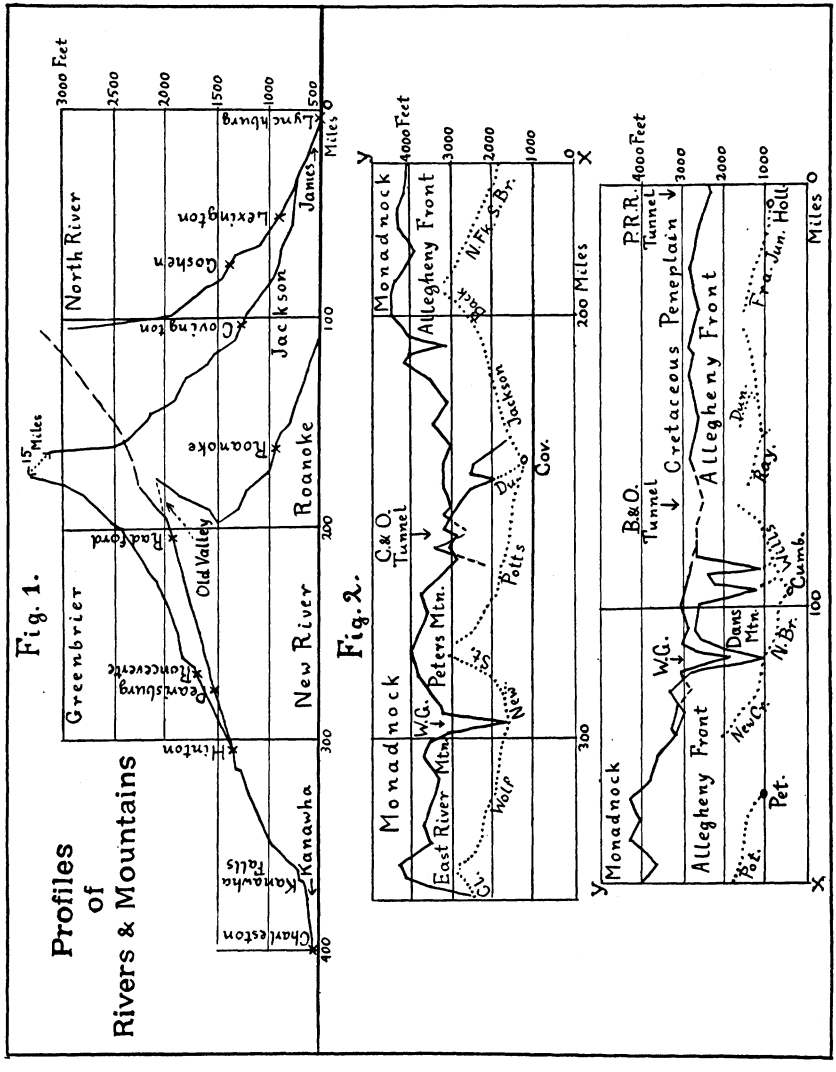


Fig. 1.
Fig. 2.
Profiles of Rivers
Havre de Grace
Harrisburg
Sunbury
Williamsport
Keating
Curwensville
Kittanning
Pittsburgh
Allegheny
Mahoning
Cush Cush
West Branch Susquehanna
Susquehanna
Feet
Miles
Shavers Fork
Cheat River
Youghiogheny
North Branch
Cumberland
Hancock
Harpers Ferry
Washington
Potomac
South Branch
Tygart Valley River
West Fork River
Monongahela
Fairmont
Clarksburg
Weston
Parsons
Elkins
Connellsville
Mt. Pleasant
Mt. Chateau
Confluence


Profiles
of
Rivers & Mountains
Fig. 1.
Greenbrier
North River
New River
Roanoke
Kanawha
Charleston
Kanawha Falls
Hinton
Fayetteville
Old Valley
Roanoke
Covington
Goshen
Lexington
Jackson
James
Lynchburg
Miles
3000 Feet
2500
2000
1500
1000
500
0
100
200
300
400
15 Miles
Fig. 2.
Monadnock
W.G.
East River Mtn.
Peters Mtn.
C. & O. Tunnel
Allegheny Front
Monadnock
4000 Feet
3000
2000
1000
0
200 Miles
300
Cov.
Potts
Jackson
N. Fk. S. Br.
B. & O. Tunnel
P.R.R. Tunnel
Cretaceous Peneplain
Dans Mtn.
Bays
Fra. Jun. Holl
Pet.
N. Br.
Willis
Cumb.
Miles
100